Warming alters root trait strategies and enchances overyielding in boreal tree seedling mixtures

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Abstract

Climate warming impacts forest ecosystems, particularly affecting plant productivity, competitive interactions, and belowground symbiotic relationships. This study investigated how moderate warming (+3°C) influences fine root traits, biomass production, and ectomycorrhizal (ECM) colonization in boreal tree seedlings (*Picea abies, Pinus sylvestris, Betula pendula, Larix sibirica*) grown both in monocultures and species mixtures. Through controlled chamber experiments using soil sourced from northern Sweden, seedlings were subjected to ambient and elevated temperature conditions for five months.

Contrary to expectations that warming enhances nutrient availability and promotes acquisitive root traits, we observed a consistent shift toward conservative root strategies across all species. Specifically, specific root length (SRL), specific root area (SRA), and root nitrogen content decreased under warming, while root carbon content (RCC) and carbon-to-nitrogen (C:N) ratio increased. These unexpected shifts suggest that seedlings prioritized structural reinforcement and longevity over rapid nutrient acquisition, likely due to lower ammonium and nitrate availability. Remarkably, biomass overyielding occurred predominantly in functionally diverse species mixtures, especially under warming. Mixtures with complementary traits, notably spruce-birch and four-species combinations, significantly exceeded monoculture productivity. Conversely, mixtures of functionally similar species underperformed, highlighting the role of niche complementarity in maximizing productivity in warmer conditions. ECM colonization was unresponsive to warming and was strongly governed by species identity and community composition rather than temperature. Despite warming, EMC colonization did not drop. That suggests trees maintained their partnership and were still functionally relevant, even under changing conditions.

These results demonstrate that warming impacts plant productivity and trait expression in ways that challenge conventional ecological assumptions. In particular, they highlight that functionally diverse species mixtures, rather than species richness alone - can support higher productivity and stable symbiotic interactions under moderate warming conditions.

Keywords: climate warming, root traits, Root Economics Space, species mixtures, boreal forest, mycorrhizal colonization, seedling productivity, niche complementarity, functional diversity, ectomycorrhizal fungi, overyielding, plant functional traits, fine root morphology, boreal tree species, experimental warming

Sammanfattning

Klimatuppvärmning påverkar skogsekosystem på flera nivåer, särskilt genom att förändra växters produktivitet, konkurrensförhållanden och symbiotiska relationer under markytan. I denna studie undersöktes hur måttlig uppvärmning (+3 °C) påverkar finrots-egenskaper, biomassa och kolonisering av ektomykorrhizasvampar (ECM) hos boreala trädplantor av gran (*Picea abies*), tall (*Pinus sylvestris),* björk (*Betula pendula*) och sibirisk lärk (*Larix sibirica*). Plantorna odlades i både monokulturer och artblandningar i klimatkammare, med jord insamlad från norra Sverige, under fem månader vid antingen ambient eller förhöjd temperatur.

I motsats till förväntningarna att uppvärmning skulle öka tillgången på näringsämnen och gynna mer exploaterande rotstrategier, observerades i stället en konsekvent förskjutning mot konservativa rotstrategier hos samtliga arter. Särskilt minskade specifik rotlängd (SRL), specifik rotarea (SRA) och kvävehalt i rötter, medan rötternas kolhalt (RCC) och kol/kväve-kvot (C:N) ökade. Dessa oväntade förändringar tyder på att plantorna prioriterade strukturell hållbarhet och livslängd framför snabb näringsupptagning, troligen på grund av lägre tillgång på ammonium och nitrat. En anmärkningsvärd upptäckt var att biomassaökning, så kallad overyielding, främst uppstod i funktionellt olika artblandningar, särskilt under uppvärmning. Blandningar med kompletterande funktionella egenskaper - framför allt gran-björk och fyrartsblandningar, visade signifikant högre produktivitet än motsvarande monokulturer. Däremot presterade blandningar av funktionellt liknande arter sämre, vilket belyser vikten av nischkomplementaritet för att maximera tillväxt under ett varmare klimat. ECM-kolonisering påverkades inte nämnvärt av uppvärmning och styrdes i hög grad av artsammansättning och artidentitet snarare än temperatur. Trots uppvärmningen minskade inte EMC-koloniseringen. Det tyder på att träd behöll sitt partnerskap och fortfarande var funktionellt relevanta, även under förändrade förhållanden.

Resultaten visar att uppvärmning påverkar växters produktivitet och egenskaper på sätt som utmanar etablerade ekologiska antaganden. Särskilt framhävs att funktionellt olika artkombinationer snarare än artantal i sig, kan stödja både hög produktivitet och stabila symbiotiska interaktioner under måttlig klimatförändring.

Nyckelord: klimatförändring, rottillväxt, Root Economics Space, artblandningar, boreal skog, mykorrhizakolonisering, plantproduktivitet, niche complementarity, funktionell mångfald, ektomykorrhizasvampar, overyielding, funktionella växtegenskaper, finrotemorfologi, boreala trädarter, experimentell uppvärmning

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Abbreviations

Abbreviations	**Definition**
AD	Average Diameter (of fine roots)
ANOVA	Analysis of Variance
C	Carbon
CNRatio	Carbon-to-Nitrogen Ratio
ECM	Ectomycorrhizal (fungi)
F	F-value (used in statistical tests such as ANOVA)
HSD	Honestly Significant Difference (Tukey's post-hoc test)
LMM	Linear Mixed-effects Model
N	Nitrogen
NH_4^+	Ammonium Ion
NO_3^-	Nitrate Ion
PCA	Principal Component Analysis
PRS®	Plant Root Simulator (ion-exchange membrane probes)
R^2	Coefficient of Determination (explained variance)
RCC	Root Carbon Content
RDA	Redundancy Analysis
RDMC	Root Dry Matter Content
RES	Root Economics Space
RFRL	Root Forks per Root Length
RLD	Root Length Density
RNC	Root Nitrogen Content
RYT	Relative Yield Total
SRA	Specific Root Area
SRL	Specific Root Length
SRTA	Specific Root Tip Abundance
S:R ratio	Shoot-to-Root Ratio

1. Introduction

Climate change is rapidly altering ecosystems across the globe (Allen et al., 2010; Anderegg et al., 2013). In the boreal forest region, temperatures are expected to increase by up to +2 to +4°C in 2100 (IPCC. 2018), which could result in shifts in soil nutrient dynamics (Pregitzer & King. 2005). These shifts in nutrient dynamics can have huge implications on plant productivity, plant-plant interactions, and plant-soil interactions. For example, in boreal forests, nitrogen availability remains a constraint on tree growth due to slow nutrient turnover in cold soils, which in turn limits forest productivity (Högberg et al., 2017; Högberg et al., 2021). However, increasing temperatures and precipitation may alleviate nitrogen limitations by stimulating soil microbial activity and nutrient mineralization rates (Rustad et al., 2001; Davidson & Janssens, 2006). While temperature-driven changes in nutrient cycling may enhance overall productivity, their effects on plant competition and resource use are often species dependent (Poorter et al., 2012; Rustad et al., 2001; Wright et al., 2004). Fine roots are a key plant response to warming, as they govern the access to soil resources by "own" nutrient uptake and /or via mycorrhizal partners (Freschet et al., 2021). Hence, plant responses to warming can be dictated by shifts in root and their traits or mycorrhizal abundances, or a combination of both, and therefore, competitive interactions (Guyonnet et al., 2018; Schenk, 2006). Further, our understanding of the mechanisms governing trait-driven responses to warming, as well as resulting effects on plant-plant and plant-soil interactions remains limited.

1.1 Plant functional traits and economic strategies

Plant traits have evolved under natural selection to optimize fitness in specific environments (Ackerly, 2003; Violle et al., 2007), and can be shaped by both biotic and abiotic factors (Reich, 2014). Trait-based ecological frameworks categorize plant strategies along continuous gradients, such as the acquisitive–conservative spectrum (Eviner, 2004; Funk et al., 2017; Reich, 2014; Weigelt et al., 2021; Westoby, 1998). Belowground, the Root Economics Space (RES) consists of plant economic tradeoffs in two trait variation dimensions, i.e. the "collaboration gradient" which represents tradeoffs between own resource acquisition (acquisitive strategy) versus dependence on mycorrhizal fungi (conservative strategy). The second dimension, the "conservation gradient" represents tradeoffs related to tissue longevity (conservative strategy) versus fast-turnover of tissue with high N content (acquisitive strategy) (Bergmann et al. 2020). Root traits can influence the relative abundances of various fungal functional guilds (Spitzer et al. 2021), as well as determine the direction and strength of plant-soil feedbacks (Spitzer et al. 2022).

In terms of root trait responses to warming, traits have been found to become more acquisitive because of increased nutrient mineralization in a permafrost, likely due to a shift to an "own nutrient acquisition" strategy (Wei et al., 2023). On the other hand, specific root length, a trait that is indicative of "own nutrient uptake" tends to be lower in warmer climates (Freschet et al., 2017). Therefore, our understanding about how traits shift with warming remains limited, and studies on warming-induced effects on root trait shifts in ecosystems such as the boreal forests are needed. Further, shifts in root traits with warming can have direct effects on soil microbial communities, which could have implications for plant nutrient uptake and productivity, as well as plant-plant interactions.

1.2 Species mixtures belowground interactions and niche complementarity

Species mixtures have been proposed as a strategy to enhance resilience and productivity in forest ecosystems (Felton et al., 2016; Jactel et al., 2018). The concept of niche complementarity suggests that species with contrasting functional traits and resource-use strategies can coexist more effectively by exploiting different niches within an ecosystem (Brassard et al., 2011; Loreau & Hector, 2001; Hooper et al., 2005). For example, species can have complementary strategies for resources such as light, water, and nutrients, thereby reducing competition and leading to higher productivity compared to monocultures (Hector et al., 1999; Tilman, 1999). Overyielding, a measure of productivity, occurs when the total biomass produced in species mixtures exceeds the sum of the biomass expected from monocultures (Beckage & Gross, 2006; Brassard et al., 2011). This enhanced productivity results from complementary interactions among species that enable more efficient resource utilization. In boreal forests, overyielding has been observed in mixtures combining fast-growing pioneer species with slower-growing species (Tilman et al., 1996, 2001; Hector et al., 1999; Loreau & Hector, 2001). Further, it has been suggested that mixed-species stands may offer greater resilience to climate change compared to monocultures (Kunstler et al., 2016), but see Hooper & Vitousek, 1997 and Huston et al., 2000. However, plant-plant interactions and temperature-induced shifts in resource partitioning can influence patterns of root allocation, where some plants may invest more in roots to compete for nutrients, while others may allocate fewer resources belowground (Blaško et al., 2020). In species mixtures, niche complementarity may further modify belowground investment, as species may divide up resources by growing roots at different depths or spreading them out differently to avoid direct competition (Casper & Jackson, 1997; Mommer et al., 2016; Turnbull et al., 2013). Warming could further lead to enhanced resource sharing among species (niche complementarity) if one species shifts to deeper rooting strategies to access more nutrients and water (Bravo-Oviedo et al., 2014; Loreau & Hector, 2001; Tobner et al., 2016). On the other hand, it could intensify belowground competition if all interacting species adopt a similar strategy (Lei et al., 2012). However, there is a paucity of studies on tree productivity in mixtures and monocultures under warming (Pretzsch 2018; Schuler et al., 2017).

1.3 Ectomycorrhizal fungi and plant-plant interactions under warming

Plant-plant interactions responses to warming might vary based on plant functional strategy or by shifts in ectomycorrhizal fungi abundances. Pioneer species such as Betula pendula generally have an acquisitive strategy by modifying specific root length (SRL) and root length density (RLD) to optimize nutrient uptake from unevenly distributed soil resources (Grime, 2002; Ostonen et al., 2011). In contrast, species such as Picea abies have a more conservative strategy by relying on extensive foraging network to compensate for nutrient scarcity (McCormack et al., 2015; Poorter et al., 2012; Weemstra et al., 2016). Under warming, higher nutrient demand could increase competition between individuals of the same species, as they would likely have similar nutrient uptake strategy and root proliferation. On the other hand, in species mixtures, species competition might be lower due to varying strategies of nutrient uptake and spatial allocation. At the same time, increased nutrient mineralization under warming might alleviate competition under warming. Further, ectomycorrhizal (ECM) fungi might affect plant-plant interactions under warming, as by forming extensive hyphal networks that help individuals to access otherwise inaccessible soil nutrients (Simard et al., 2012; van der Heijden et al., 2015). The level of investment in ECM fungi varies between monocultures and mixed-species forests, shaping both biomass distribution and competition between species (Bent et al., 2011; Otsing et al., 2021). In monocultures, reliance on shared fungal networks may intensify competition for similar soil resources. In contrast, in mixed-species stands, species-specific fungal associations or differential use of hyphal networks can partition nutrient access, enabling complementary resource use and stabilizing coexistence dynamics. Despite the potential for fungal-mediated niche partitioning, it remains unclear how warming influences ECM fungal abundance and function, with studies reporting both positive and variable responses (Mohan et al. 2014; Bennett & Classen, 2020; de Carlan et al. 2024), and shifts in mycorrhizal abundances in monocultures versus species mixtures under warming is not understood. Understanding these plant-fungal interactions may be important for predicting forest resilience under climate change, particularly as rising temperatures alter soil nutrient availability and carbon cycling (Terrer et al., 2016).

1.4 Research objectives and hypotheses

By analyzing root traits for monocultures, biomass allocation, and ECM colonization both monocultures and mixed forests under warming conditions, this study aims to investigate how species-specific root strategies affect overyielding in early seedling growth dynamics, shaping the long-term forest productivity. This thesis aims to improve our understanding of how plant-plant interactions (i.e. in monocultures or species mixtures) and mycorrhizal colonization respond to warming. To do so, we focus on the boreal biome, a forest zone covering roughly 30% of the world's forest area and storing nearly one-third of all terrestrial carbon (Bradshaw & Warkentin, 2015). Particularly in Sweden, a large proportion of forests is managed (Högberg et al., 2021; Nilsson et al., 2010), and forests are dominated by Norway spruce (Picea abies) and Scots pine (Pinus sylvestris), which together contribute approximately 80% of the standing forest volume and silver birch (Betula pendula) with smaller contributions (Nilsson et al., 2021). In this study, we focus on these species, as well as Larix sibirica, which might be planted more in the future (Skogsstyrelsen. 2019).

Hypotheses

In my thesis, I tested the following hypotheses:

H1: In single species treatments, fine root traits will reflect an acquisitive strategy under warming, driven by increased nutrient availability.

H2: Total plant biomass will be higher in mixed-species treatments compared to single species under both temperature treatments, as niche complementarity enables efficient resource use and maximizes soil and light capture.

H3: Mycorrhizal colonization will be higher in single-species treatments compared to mixtures due to stronger intraspecific competition for nutrients, particularly under ambient temperature conditions. Under elevated temperature, we expect colonization to decrease due to increased nutrient mineralization alleviating nutrient stress and reducing the plant's reliance on symbiotic fungi.

2. Material & Method

2.1 Experimental set-up

The study was conducted using soil sourced from an established common garden experiment at Svartberget, near Vindeln in northern Sweden (64°15′N, 19°47′E). This experimental garden was originally established to assess physiological and growth responses of key boreal tree species under natural conditions. Soil was systematically collected from monoculture plots of *Larix sibirica, Picea abies, Pinus sylvestris, and Betula pendula*, including the microbial communities typically associated with each species. Soil samples were bulked, sieved (Ø 2 mm), thoroughly homogenized, and subsequently mixed with sand at a 50:50 ratio to standardize texture, optimize drainage, and closely mimic natural forest floor conditions.

The experimental design included four single-species treatments, six two-species mixtures, and one four-species mixture to investigate the effect of species diversity on tree productivity and fine root traits under warming conditions (Fig. 1). Treatments were replicated across eight blocks and randomly assigned to two temperature regimes: ambient temperature 15°C and elevated temperature 18°C. Seedlings were planted individually or in designated mixtures in 3-liter pots, maintaining consistent soil volume and planting methods. A total of 175 experimental units were established (one additional unit was omitted due to planting error). Controlled climate chambers were used to simulate warming conditions. To minimize potential chamber effects, pots were rotated between chambers and within block once during the experiment. The experiment lasted five months to allow sufficient observation time for interactions and responses to temperature treatments.

Throughout the experimental period, pots were watered every three days and volume was administered as needed. Thereby eliminating water availability as a confounding factor and isolating temperature as the sole variable under investigation.

Experimental treatments included:

1. Spruce (Picea abies)
2. Larch (Larix sibirica)
3. Pine (Pinus sylvestris)
4. Birch (Betula pendula)
5. Spruce + Larch
6. Spruce + Pine
7. Spruce + Birch
8. Larch + Pine
9. Larch + Birch
10. Pine + Birch
11. Four-species mixture (Birch + Larch + Spruce + Pine)

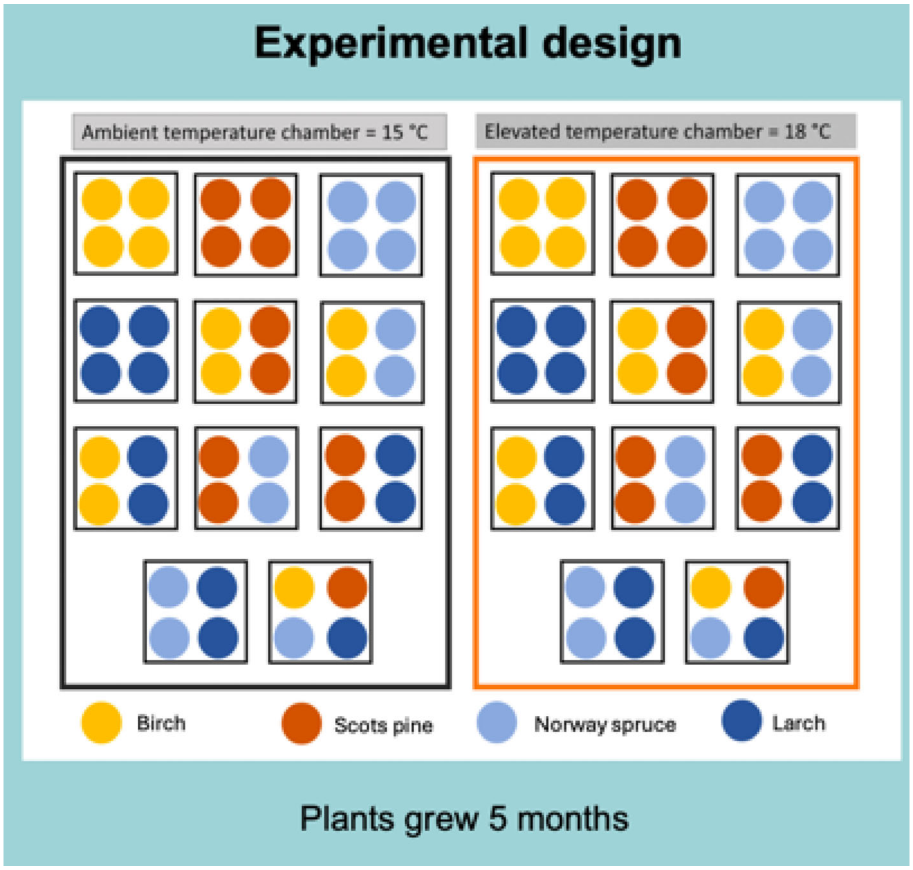


Figure 1. Conceptual figure on species combination and the mixture types for this study.

2.2 Plant and soil measurements

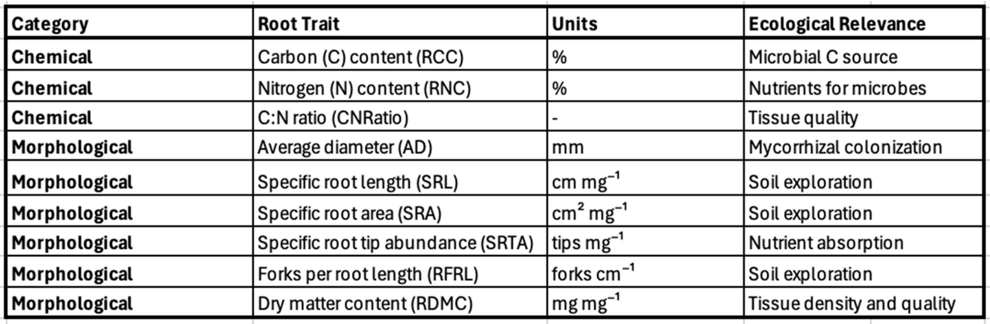
At the end of the five-month experiment, seedlings were harvested and dried to determine biomass. Measurements recorded included aboveground biomass (shoot dry weights and average plant height per pot) and belowground biomass (fine roots, coarse roots, and total root biomass).

Root samples from single-species treatments were carefully washed to remove soil particles and debris, then scanned using WinRhizo software (Version 2016, Regent Instruments, Quebec, Canada) at 800 dpi. The morphological root traits measured included specific root length (SRL), specific root area (SRA), average diameter (AD), specific root tip abundance (SRTA), forks per root length (RFRL), and root dry matter content (RDMC) (Table 1). Following scanning, roots were dried at 65°C for 48 hours, weighed, and ground using a ball mill. Root carbon (C), nitrogen (N), and carbon-to-nitrogen ratio (CNRatio) were determined by dry combustion using an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific).

Mycorrhizal colonization intensity was determined by microscopically examining root tip closest to 100 grid intersections on the plate per sample at 20× magnification following a modified protocol from Karst et al. (2021). Root tips were classified as colonized if they displayed at least two of the following characteristics: swollen appearance, absence of root hairs, and non-transparent tissue. Colonization was further verified by confirming the presence of a fungal mantle and Hartig net structure under a compound microscope at 200× magnification for a subset of samples. Additionally, the presence of rhizomorphs was recorded as a binary indicator (yes/no) for each sample.

To quantify soil nutrient availability, Plant Root Simulator (PRS®) probes (Western Ag, Canada) containing ion-exchange membranes were installed in each pot at the start of the experiment and retrieved at its conclusion. These probes continuously measured supply rates of cationic and anionic nutrients (macro- and micronutrients). After five months, probes were analyzed externally by Western Ag following standardized protocols (Ochoa-Hueso et al., 2023).

Table 1. Fine root traits, units and their ecological relevance (Spitzer et al., 2021).



Category	Root Trait	Units	Ecological Relevance
Chemical	Carbon (C) content (RCC)	%	Microbial C source
Chemical	Nitrogen (N) content (RNC)	%	Nutrients for microbes
Chemical	C:N ratio (CNRatio)	-	Tissue quality
Morphological	Average diameter (AD)	mm	Mycorrhizal colonization
Morphological	Specific root length (SRL)	cm mg^{-1}	Soil exploration
Morphological	Specific root area (SRA)	cm^2 mg^{-1}	Soil exploration
Morphological	Specific root tip abundance (SRTA)	tips mg^{-1}	Nutrient absorption
Morphological	Forks per root length (RFRL)	forks cm^{-1}	Soil exploration
Morphological	Dry matter content (RDMC)	mg mg^{-1}	Tissue density and quality

Figure 2. Greenhouse study, ambient and elevated pots of single species. [photography: O. Andersson]

Figure 3. Cleaned roots. Left is a four-mixture, right is two-species mixture of birch+pine. [photography: O. Andersson]

2.3 Statistical analysis

Statistical analyses were conducted using R software (version 4.4.1). Normality was assessed using Shapiro–Wilk tests and quantile–quantile (QQ) plots; non-normally distributed variables were log-transformed. Linear mixed-effects models (LMM) assessed temperature and mixture effects on biomass, morphological, and chemical traits, with block included as a random factor. Analysis of variance (ANOVA) followed by post-hoc Tukey's HSD tests compared differences among treatments. Paired t-tests were employed for within-species trait differences due to warming. Statistical significance was set at $p \leq 0.05$.

Principal Component Analysis (PCA) using standardized trait values summarized multivariate variation across species and treatments. PCA allowed visualization and exploration of trait patterns aligned with the Root Economics Space (RES) framework, identifying major axes of acquisitive-conservative resource use strategies (Matthus et al., 2025; Reich et al., 2014).

To isolate the influence of nutrients and temperature on root traits, redundancy analysis (RDA) and partial RDA were performed using the *vegan* package. Standard RDA identifies variation in multivariate responses (root traits) explained by predictors (soil nutrients, temperature). Partial RDA further conditions out nuisance variables such as block or treatment, isolating the unique contribution of the variables of interest (Legendre & Legendre, 2012).

RDA model:

$$\boldsymbol{X_{traits} = Y_{environment} + residuals}$$

Partial RDA model:

$$\boldsymbol{X_{traits} = Y_{environment} + Condition(Z_{blocks,treatments}) + residuals}$$

Where:

- X_{traits} is the matrix of response variables (root traits).
- $Y_{environment}$ explanatory variables (nutrients or temperature).
- $Z_{blocks,treatment}$ covariates (blocking or experimental layout factors).
- $Residuals$ represent unexplained trait variation.

This approach isolates environmental factors' unique explanatory contributions, removing variance associated with blocking or treatment design.

2.3.1 Relative Yield Total (RYT) Calculation

To assess the productivity outcomes of species mixtures relative to monocultures, the Relative Yield Total (RYT) were calculated for each mixed-species treatment. RYT is a widely used index in biodiversity-ecosystem functioning studies to quantify overyielding, the phenomenon where species mixtures produce more biomass than expected based on their monoculture performance (Trenbath, 1974; Loreau & Hector, 2001).

RYT is defined as the sum of the relative yields of each species in the mixture, where relative yield is calculated as the biomass of a species grown in mixture divided by its biomass in monoculture. Mathematically, for a mixture of n species:

$$RYT = \sum_{i=1}^{n} \frac{Y_{mix(i)}}{Y_{mono(i)}}$$

Where $Y_{mix(i)}$ is the observed biomass of species i in mixture and $Y_{mono(i)}$ is the mean biomass of that species when grown in single species pots. An RYT value greater than 1 indicates **overyielding,** implying that species interactions in the mixture led to higher total productivity than would be expected based on their monoculture performances. Expected monoculture yields were calculated within the same block and treatment conditions, ensuring accurate and context-specific comparisons (Hooper and Dukes, 2004; Jolliffe, 2000).

3. Results

3.1 Fine root trait variation

Principal Component Analysis (PCA) revealed distinct gradients of variation in fine root morphological and chemical traits across species and temperature treatments (Figure 4). The first principal component (PC1) explained 60.2% of total variance and was primarily associated with a resource conservation gradient, dominated by root carbon content (RCC) and carbon-to-nitrogen ratio (CNRatio). The second axis (PC2, 25.1%) reflected nutrient acquisition traits, including specific root length (SRL), specific root area (SRA), and root nitrogen content (RNC), separating acquisitive vs. conservative root strategies. Species were broadly separated along these axes: Norway spruce exhibited high SRL SRA and RNC values, suggesting acquisitive traits, while birch expressed a high CNRatio and RDMC, reflecting a conservative strategy. Larch and pine were characterized by thicker roots relative to the other species, and generally had higher values of N content under ambient temperatures, which shifted under warming.

3.1.1 Trait responses to elevated temperature

To evaluate Hypothesis 1, which predicted that warming would drive fine root traits toward more acquisitive strategies, we assessed trait responses across and within species under elevated temperature (+3 °C) conditions.

A separately partial redundancy analysis (partial RDA) was performed with temperature treatment as the sole explanatory variable and block as a covariate. The model was statistically significant ($F = 13.49$, $p < 0.001$), with RDA1 capturing 100% of the constrained variation. Warming alone explained 17.8% of the variation in root traits (adjusted $R^2 = 0.1674$), after accounting for block effects.

Trait-wise ANOVAs confirmed significant cross-species reductions in specific root length (SRL; $F = 18.24$, $p < 0.001$), specific root area (SRA; $F = 19.60$, $p < 0.001$), and root tissue surface area (SRTA; $F = 14.21$, $p < 0.001$) under elevated temperature. Root nitrogen content (RNC) also declined significantly ($F = 5.50$, $p = 0.022$), while root carbon content (RCC; $F = 12.29$, $p = 0.001$) and carbon-to-nitrogen ratio (CNRatio; $F = 5.99$, $p = 0.017$) both increased. Root dry matter content (RDMC) increased non-significantly ($F = 1.63$, $p = 0.207$). Root average diameter (AD; $F = 0.003$, $p = 0.957$) and root fork length (RFRL; $F = 0.037$, $p = 0.848$) remained stable (see Table 1 and Supplementary Figure S1).

At the species level, Norway spruce consistently exhibited the highest SRL and SRA values ($F = 17.29$, $p = 0.0003$) across both treatments, while Siberian larch and Scots pine displayed the strongest trait shifts under warming ($F = 17.11$, $p = 0.004$). For instance, paired t-tests confirmed significant within-species declines in SRL and SRA ($p < 0.001$ for both) in larch and pine (Supplementary Table S2 and Figure S2). These species also experienced the largest decreases in RNC and largest increases in CNRatio and RCC. Notably, CNRatio increased by +10.3 units in larch ($p < 0.001$) and +9.55 in pine ($p < 0.001$), while RCC increases were strongest in larch and pine ($F = 10.16$, $p < 0.001$).

3.1.2 Trait responses to soil nutrient availability under warming

To isolate the role of nutrient availability, a partial RDA was conducted with 14 nutrient predictors, conditioned on both treatment and block (Figure 5B). The model explained 36.3% of total trait variation (adjusted $R^2 = 0.240$), with RDA1 accounting for 87.2% of constrained variance and RDA2 for 7.5%.

Permutation-based ANOVA confirmed the model's significance ($F = 2.475$, $p = 0.001$). Among predictors, NH_4^+ ($F = 17.28$, $p < 0.001$) and NO_3^- ($F = 9.29$, $p < 0.001$) were the most influential nutrients, with boron (B, $F = 3.11$, $p = 0.065$) and sulfur (S, $F = 2.70$, $p = 0.083$) approaching significance.

Root traits aligned with nutrient enrichment included SRL, SRA, RNC, and SRTA, which were positively correlated with NH_4^+ and NO_3^- (Pearson's $r = 0.29$ to 0.56, all $p < 0.05$; see Supplementary Figure S3). In contrast, CNRatio, RDMC, and RCC were negatively correlated with N availability, suggesting that higher nutrient availability promoted acquisitive traits, while nutrient depletion under warming fostered conservatism (see Table 2 and Supplementary Figure S3 for correlation coefficients and p-values).

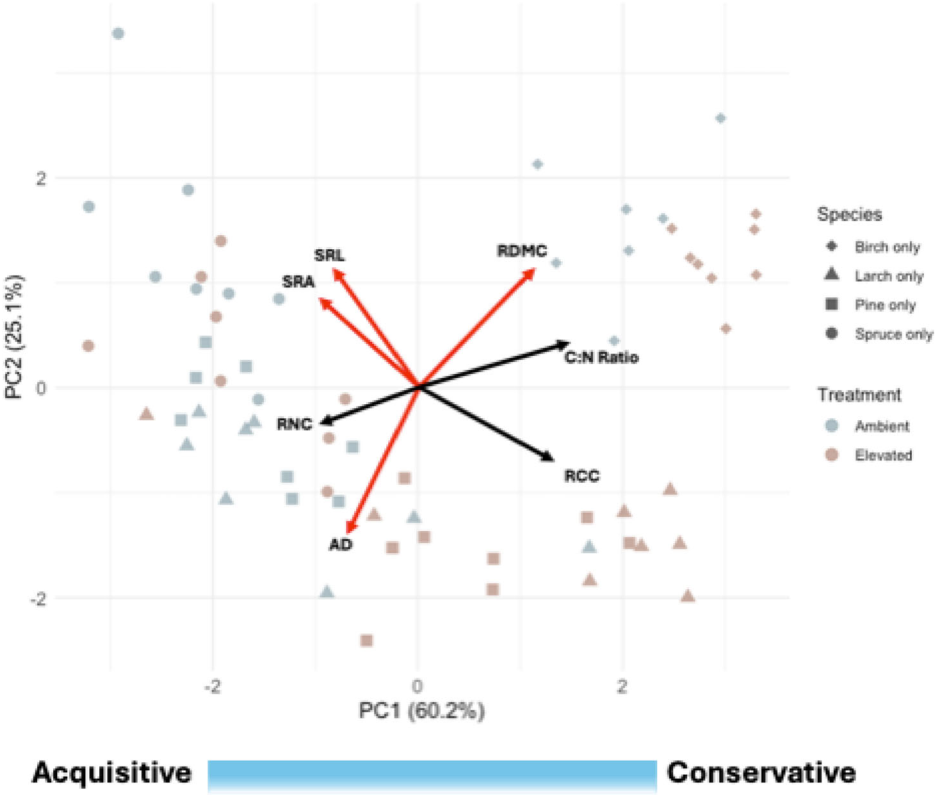


Figure 4. Principal Component Analysis (PCA) of fine root traits. PCA of morphological and chemical root traits for all single-species pots under ambient and elevated temperatures. Points are colored by temperature treatment and shaped by species identity (Birch, Larch, Pine, and Spruce). Trait vectors superimposed on the PCA ordination showing the contribution of each trait to the observed variation. PC1 (60.2%) represents a conservation gradient (RCC, CNRatio), while PC2 (25.1%) reflects nutrient acquisition strategies (SRL, SRA, RNC). Conservative trait syndromes were more common under warming (brown), while acquisitive profiles dominated under ambient conditions (blue). Data points represent individual species-treatment combinations, with species-specific clustering indicating functional differences in root strategies.

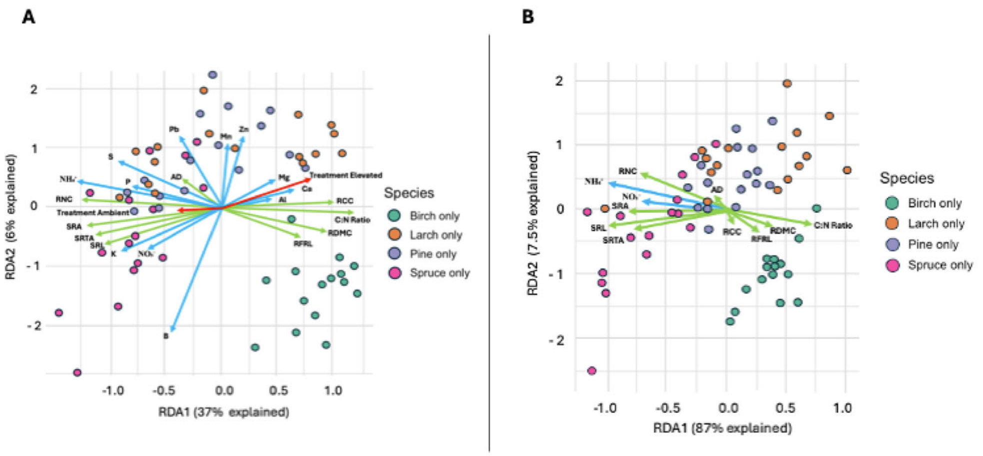
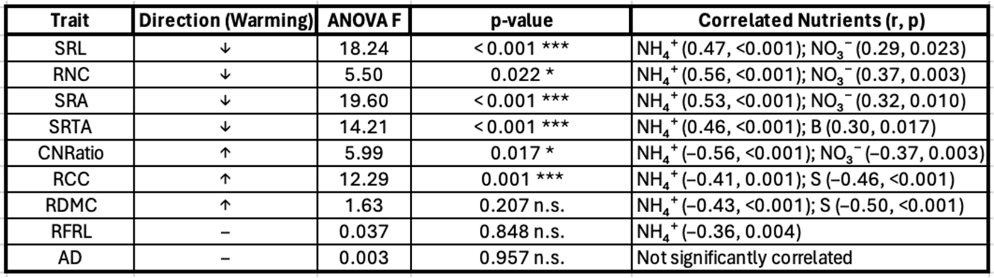


Figure 5. Redundancy Analysis (RDA) and Partial RDA of root trait–environment relationships. (A) RDA biplot showing the relationship between root traits (green arrows), environmental predictors (blue arrows), and species identity (color-coded points) across ambient and elevated treatments. RDA1 (37%) was driven primarily by temperature and inorganic nitrogen availability (NH_4^+, NO_3^-), while RDA2 (6%) captured more variable micronutrient effects. (B) Partial RDA conditioned on treatment and block, isolating the influence of nutrient availability on root traits. RDA1 (87.2%) captured the dominant variation in trait–nutrient relationships. The ordination reveals strong alignment of acquisitive traits (SRL, RNC, SRA, SRTA) with N availability, and conservative traits (CNRatio, RCC, RDMC) with low nutrient supply.

*Table 2. Table summarizing direction and significance of temperature-driven trait changes (based on ANOVA), alongside Pearson correlation coefficients (r) with major nutrients. Traits with significant responses to elevated temperature include SRL, SRA, SRTA, RNC, RCC, and CNRatio. NH_4^+ and NO_3^- were the strongest predictors of trait variation. RDMC showed a non-significant trend toward increase, while AD and RFRL remained unchanged. Nutrient correlation coefficients are reported with significance thresholds; asterisks denote statistical significance (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. = not significant).*



Trait	Direction (Warming)	ANOVA F	p-value	Correlated Nutrients (r, p)
SRL	↓	18.24	< 0.001 ***	NH_4^+ (0.47, <0.001); NO_3^- (0.29, 0.023)
RNC	↓	5.50	0.022 *	NH_4^+ (0.56, <0.001); NO_3^- (0.37, 0.003)
SRA	↓	19.60	< 0.001 ***	NH_4^+ (0.53, <0.001); NO_3^- (0.32, 0.010)
SRTA	↓	14.21	< 0.001 ***	NH_4^+ (0.46, <0.001); B (0.30, 0.017)
CNRatio	↑	5.99	0.017 *	NH_4^+ (–0.56, <0.001); NO_3^- (–0.37, 0.003)
RCC	↑	12.29	0.001 ***	NH_4^+ (–0.41, 0.001); S (–0.46, <0.001)
RDMC	↑	1.63	0.207 n.s.	NH_4^+ (–0.43, <0.001); S (–0.50, <0.001)
RFRL	–	0.037	0.848 n.s.	NH_4^+ (–0.36, 0.004)
AD	–	0.003	0.957 n.s.	Not significantly correlated

3.2 Biomass responses to warming and species mixtures

To evaluate Hypothesis 2, which predicts that mixed-species treatments will enhance total biomass production via niche complementarity. We further explored the effects of temperature and species mixture type on Relative Yield Total (RYT) (see Figure 6).

3.2.1 Effects of temperature on total biomass and biomass allocation for individual species and species mixtures

Elevated temperature significantly increased total biomass across all mixture types (ANOVA: $p < 0.001$, Figure 7 and Fig. S5), as well as biomass allocation patterns (Figures S6-S9). All species had a significant increase in shoot biomass (Table S3) with warming, as well as mixtures with spruce and larch and spruce and birch. Total root biomass was significantly higher in four species mixtures under warming relative to two-species and single species mixtures (Table S3; Fig. S8A and B). Further, pots with spruce only or pine only, as well as in mixtures with birch and pine, and birch and spruce also had significantly higher total root biomass under warming. These patterns were similar for fine root biomass allocation, except those mixtures with larch and pine also had a significant increase in fine root biomass with warming (Table S3; Fig. S9B).

Species composition had a significant effect on the shoot-to-root ratio (S:R ratio), (LMM: $\chi^2 = 56.95$, df = 10, $p < 0.001$). which represents the balance between aboveground (shoots) and belowground (roots) biomass (Figure S10A and S10B). A higher S:R ratio indicates preferential investment in shoot growth, often in response to competition for light, whereas a lower ratio reflects increased investment in roots. Spruce-only (mean difference = 0.3586, $p < 0.0001$) and Spruce+Larch (mean difference = 0.259, $p < 0.001$) had significantly higher S:R ratios than Birch-only, Spruce+Birch, and Larch+Birch (Figure S10A). Elevated temperature had no significant effect on S:R ratio in LMM ($p = 0.2055$; Figure S10B). We also found significant differences in height between single-species and mixed-species treatments under warming Figure S6A and S5B) and this varied by species (Table S3).

3.2.2 Effects of species mixtures and warming on contributions to Overyielding (RYT)

Relative yield total (RYT) exceeded 1 for both two-species and four-species mixtures under warming, which indicates overyielding ($F = 48.75$, $p < 0.001$). Mixture type significantly influenced overyielding ($F = 25.54$, $p < 0.001$), with four-species mixtures exhibiting higher RYT than two-species mixtures. However, Tukey's HSD post-hoc test indicated that this difference was marginally insignificant (p = 0.061), suggesting a weak but non-definitive trend toward greater overyielding in four-species mixtures (Figure 6). There was no significant interaction between warming and mixture type (F = 0.151, p = 0.698), while mixture type influences RYT, warming enhances overyielding similarly in both two-species and four-species mixtures.

Mixtures with significant overyielding were Spruce and Birch (RYT = 1.54, p < 0.001) and the four-species mixture (RYT = 1.47, p < 0.001; Figure S3). Further, some mixtures showed moderate overyielding such as Spruce and Larch (RYT = 1.23, p > 0.0504) and Spruce and Pine (RYT = 1.04, p > 0.141) but these responses were not statistically significant (Figure S4).

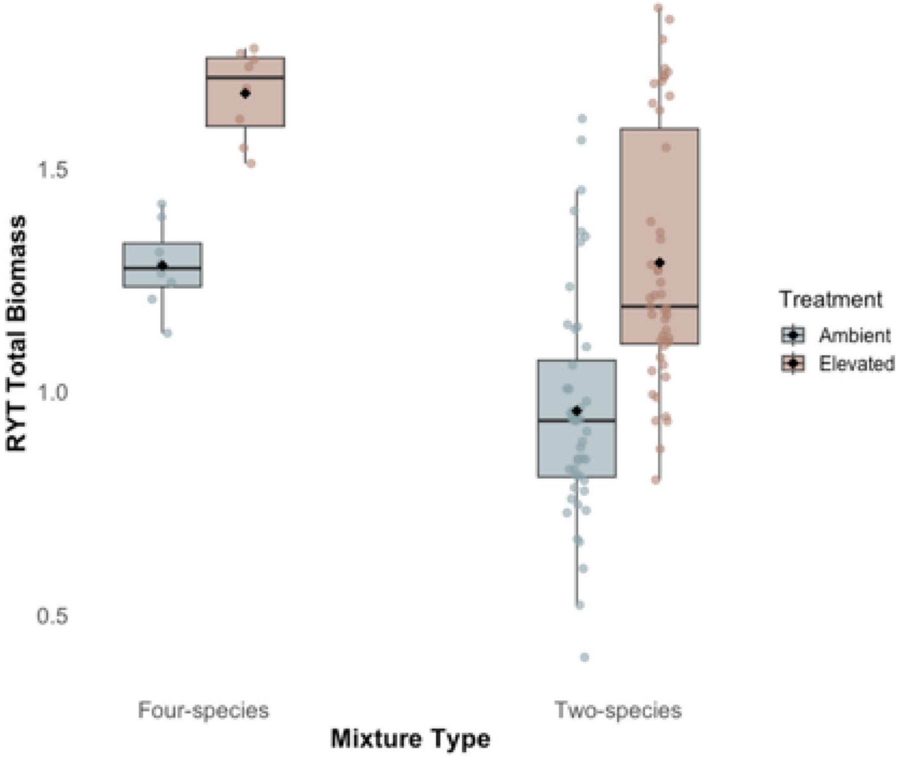


Figure 6. Interaction of treatment and mixture type on Relative Yield Total (RYT) across different mixture types (single-species, two-species, and four-species) under ambient (blue) and elevated (brown) temperature treatments. RYT was calculated as the sum of the observed-to-monoculture yield ratios for each species within a mixture (see Methods). An RYT > 1 indicates overyielding, whereas RYT < 1 indicates underyielding. Boxplots display the median. Black diamonds represent treatment means.

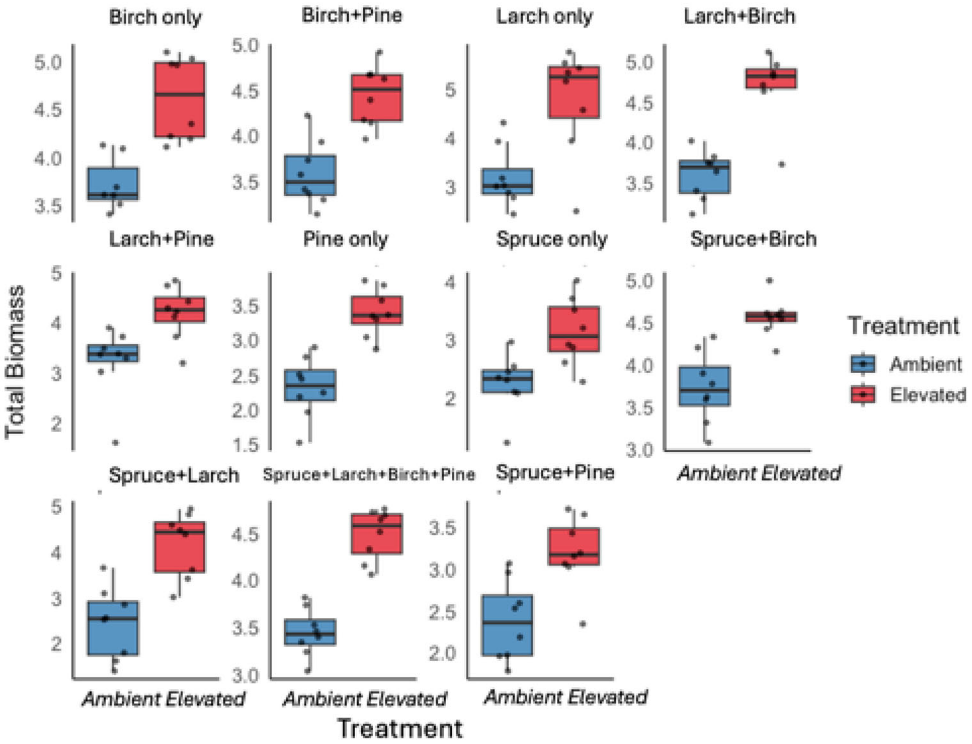


Figure 7. Total biomass boxplots display species-specific total biomass responses under ambient (blue) and elevated (red) temperature treatments across single- and mixed-species treatments. Biomass is the sum of shoot and root biomass (log-transformed for normalization). Data points represent individual observations.

3.3 Mycorrhizal colonization in response to species mixture and warming

To evaluate Hypothesis 3, which hypothesized that mycorrhizal colonization would be higher in single-species treatments compared to mixtures due to increased competition for nutrients in monocultures. We additionally analyzed the effects of species identity, mixture type, and temperature on percentage mycorrhizal colonization.

3.3.1 Effects of mixture type and warming on mycorrhizal colonization

Warming did not have a significant effect on percentage mycorrhizal colonization ($F = 0.105$, $p = 0.746$; Figure 8). However, mycorrhizal colonization differed significantly across species and mixture types ($F = 32.82$, $p < 0.001$). We found a marginally insignificant difference in colonization between single species and four-species mixtures ($F = 3.209$, $p = 0.055$). Two-species mixtures did not significantly differ from single species and four-species mixtures ($p = 0.1859$ and $p = 0.3777$). Pairwise comparisons revealed that species mixtures displayed diverse colonization responses (Figure 9 and S11). Spruce+Birch ($p < 0.0001$) and Larch+Birch ($p < 0.0001$) exhibited significantly higher colonization than other species combinations. Conversely, Larch+Pine ($p < 0.0001$) and Spruce+Larch ($p < 0.0001$) mixtures showed significantly lower colonization than Birch-only ($p < 0.0001$).

Species identity was the dominant driver of colonization (Chisq = 401.13, $p < 2.2e-16$), with block effects accounting for experimental variability but not altering the significance of species effects (variance = 31.23). Birch-only treatments exhibited the highest colonization, with significantly greater fungal associations than Larch-only ($p < 0.001$) and Pine-only treatments ($p < 0.001$, Figure 6 and S9). In contrast, Spruce-only treatments had significantly lower colonization than Pine-only ($p < 0.001$).

A further breakdown of treatment effects within each species and species combination revealed that the impact of warming on mycorrhizal colonization remained non-significant across all groups (Figure S9). For all species and species combinations, p-values were greater than 0.05, indicating no significant effect of treatment (Ambient vs. Elevated) on mycorrhizal colonization. Some species combinations, such as Larch+Birch ($F = 1.32$, $p = 0.2705$) and Spruce+Larch ($F = 0.77$, $p = 0.3978$), exhibited relatively larger F-values compared to others, but these values were still not statistically significant. Overall, there is no evidence that warming influences mycorrhizal colonization across the tested species and species combinations (Figure S11).

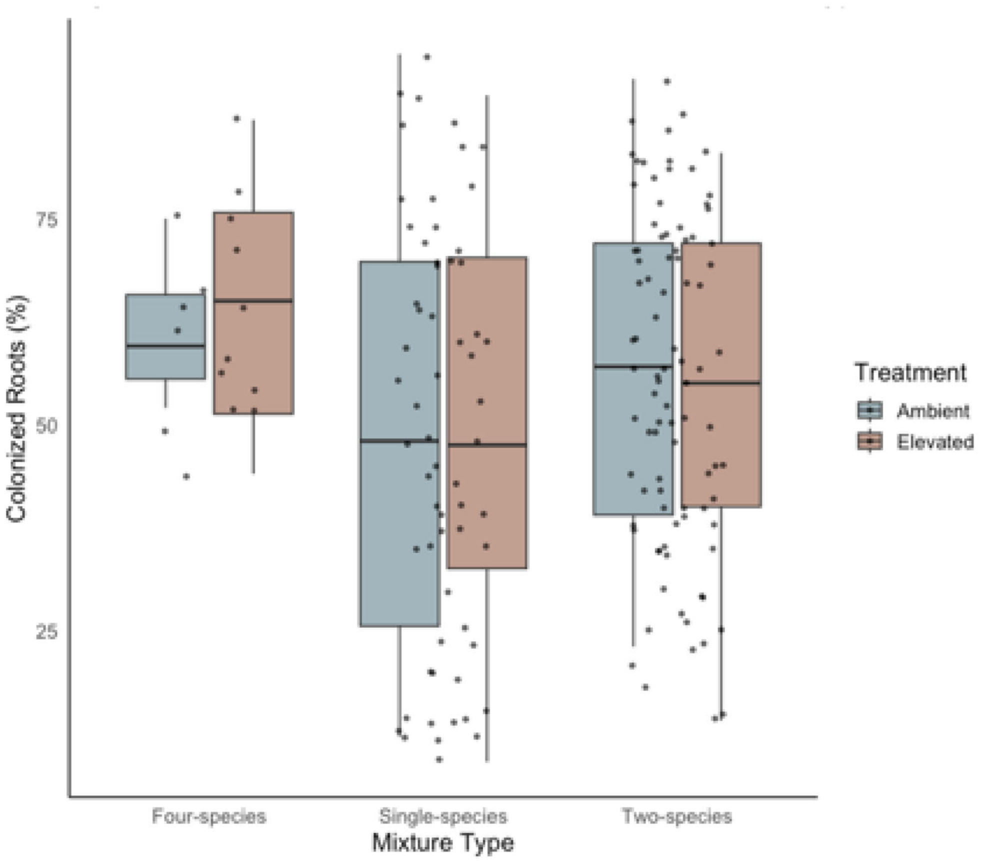


Figure 8. Mycorrhizal colonization (% colonized roots) across single-species, two-species, and four-species mixtures under ambient (blue) and elevated (brown) temperature treatments.Boxplots display the median, interquartile range, and individual data points. ANOVA results showed significant species and mixture type effects ($p < 0.001$), but no significant temperature effects ($p = 0.746$) or temperature × mixture type interactions ($p = 0.927$). Tukey's HSD post-hoc tests revealed that four-species mixtures exhibited the highest median colonization, while single-species treatments displayed the lowest median colonization, though the difference was only marginally significant ($p = 0.0555$). Data points represent individual sample measurements.

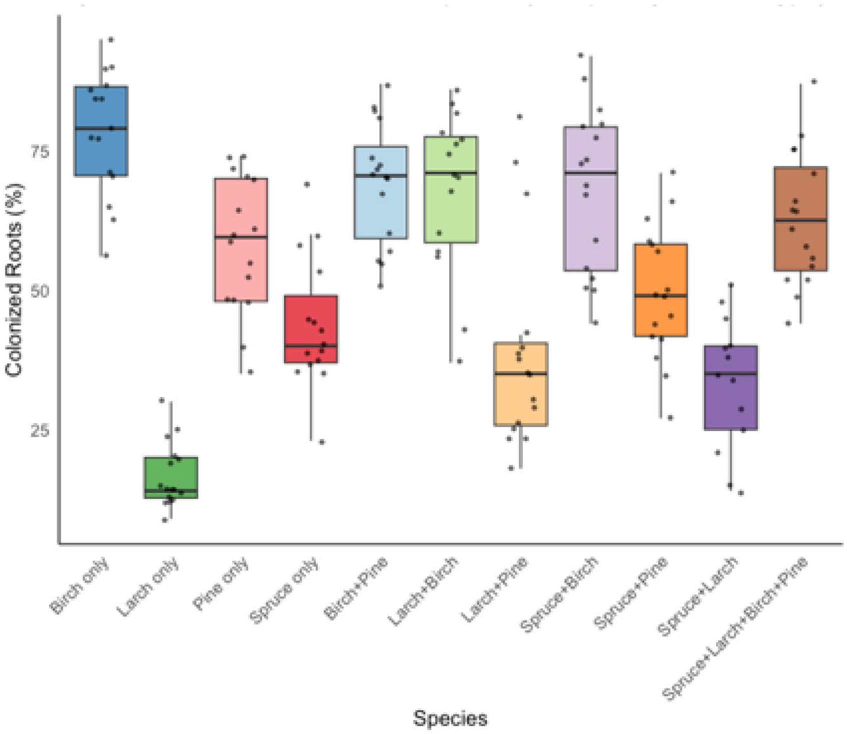


Figure 9. Mycorrhizal colonization rates for individual species, grouped by mixture type showing mycorrhizal colonization varied significantly among species (ANOVA: $p < 0.001$), with Birch-only treatments exhibiting the highest colonization and Larch-only the lowest. Tukey's HSD post-hoc tests showed significantly greater colonization in Birch-only treatments compared to Larch-only ($p < 0.0001$) and Pine-only ($p = 0.0009$). Spruce-only had significantly lower colonization than Pine-only ($p = 0.000065$). Species-specific interactions influenced colonization patterns, with Spruce+Birch and Larch+Birch showing significantly higher colonization than Larch+Pine and Spruce+Larch ($p < 0.0001$). Data points represent individual sample values.

4. Discussion

4.1 Fine root trait shifts indicate conservative strategies under warming

The first hypothesis predicted that fine root traits would shift toward more acquisitive strategies under elevated temperature, driven by enhanced nutrient mineralization. Contrary to this expectation, we observed consistent shifts across species toward more conservative trait expressions under warming. Specifically, traits along both the conservation (Root N–RTD) and collaboration (SRL–AD) gradients of the Root Economics Space (RES) shifted toward resource conservation: specific root length (SRL), specific root area (SRA), and root nitrogen concentration (RN) all decreased, contradicting trends typically reported in field-based warming studies (Wei et al., 2023; Wang et al., 2021). While root carbon content (RCC) and C:N ratio increased. These findings suggest a strategic reallocation of resources toward traits associated with longer lifespan, higher structural investment, and greater carbon retention, hallmarks of a conservative root phenotype (Freschet et al., 2018; Reich, 2014; Matthus et al., 2025). This conservative shift aligns closely with recent meta-analyses highlighting that acquisitive species generally achieve high growth potential only under ideal nutrient-rich conditions, whereas conservative species often outperform acquisitive counterparts under the stressful conditions characteristic of boreal forests, as they more effectively maintain stable growth rates under nutrient scarcity and environmental stress (Augusto et al., 2025).

Root trait responses to warming have been hypothesized to be driven by nutrient availability, resulting in plant shifts in belowground resource acquisition by increasing specific root length and specific root area to maximize nutrient uptake efficiency (Pregitzer et al. 2002; Liu et al. 2015; Ostonen et al. 2011, 2017). The closed system of our pot experiment, with finite soil volume and no nutrient replenishment, likely led to progressive nutrient depletion, rather than enrichment (Hutchings & de Kroon, 1994; McNickle & Cahill, 2009). RDA and correlation heatmaps, which collectively reveal that elevated temperature led to a decline in nutrient-acquisitive traits, despite evidence that NH_4^+ and NO_3^- were associated with increased foraging capacity. This suggests that warming may indirectly reduce trait expression via nutrient depletion over time. The spatial proximity of "TreatmentElevated" to CNRatio, RCC, and RDMC vectors in the RDA plot (Figure 5A), alongside weak alignment with nutrient vectors in Figure 5B, supports this interpretation. These patterns point to a functional decoupling between nutrient availability and temperature-induced trait responses, whereby temperature overrides nutrient signals, promoting structurally conservative strategies to buffer nutrient scarcity.

Ecologically, increased C:N ratio and RCC, coupled with declines in SRL and RN, are consistent with a deeper rooting strategy aimed at enhancing access to slowly cycling nutrients in deeper soil layers. Although our pots limited vertical rooting depth, previous literature suggests that higher RTD and lower SRL may promote steeper rooting angles and greater mechanical strength, enabling roots to penetrate compacted substrates or explore deeper soil strata under nutrient stress (Matthus et al., 2025; Weemstra et al., 2016). This interpretation highlights the potential for conservative trait shifts to reflect not only reduced foraging intensity but also altered rooting architecture, which warrants further study in field-based systems.

Interestingly, average root diameter (AD) remained stable across treatments, suggesting evolutionary or functional constraints that preserve compatibility with ectomycorrhizal colonization or maintain efficient hydraulic conductance (Valverde-Barrantes et al., 2017; Matthus et al., 2025). Similarly, mycorrhizal colonization did not change significantly with temperature, possibly indicating a trade-off where plants maintain fungal associations while shifting carbon investment away from root morphology toward structural reinforcement.

Species-level patterns refined the broader response. Spruce maintained high SRL but showed limited trait plasticity, suggesting conservative buffering or low morphological flexibility. In contrast, Siberian larch and Scots pine showed the largest trait shifts, including declines in SRL and RNC and increases in RCC and CNRatio (Table S2), signaling strong plasticity under warming-induced nutrient limitation (Birouste et al., 2014). Birch occupied an intermediate position, maintaining high C:N ratios while expressing moderate morphological changes, aligning with a generalist strategy balancing acquisitive and conservative functions. Taken together, these findings support established ecological theory, where trait shifts toward conservatism enhance survival and growth stability under nutrient-limited, warming environments (Freschet et al., 2017; Hartmann et al., 2020).

4.2 Biomass overyielding in mixed-species pots

Consistent with our second hypothesis, mixed-species treatments demonstrated significant biomass overyielding compared to monocultures. Under elevated temperatures, both two-species and four-species mixtures consistently exhibited overyielding (RYT > 1), while under ambient conditions, only four-species mixtures achieved overyielding. These findings support an extensive body of research indicating productivity benefits in mixed- species stands, typically attributed to improved resource utilization through functional diversity (del Río et al., 2021; Liang et al., 2016; Pretzsch & Schütze. 2021). For example, del Río et al. (2021) highlighted that complementary use of canopy and root space among species in mixed forests often facilitates more efficient resource capture, enhancing overall stand productivity.

Notably, although our experimental design did not directly measure niche complementarity, mixtures including spruce and birch, along with the four-species combinations, demonstrated pronounced overyielding, indicating that distinct functional traits and resource-use strategies likely enabled effective exploitation of complementary niches. Conversely, mixtures like larch and pine exhibited underyielding, likely due to functional redundancy, where overlapping ecological traits intensify competition rather than facilitate resource partitioning (Tilman et al., 1997; Hooper & Vitousek, 1997). Such observations align with findings from Ruiz-Peinado et al. (2021), who reported limited productivity gains in mixtures of species with similar ecological strategies due to competitive rather than complementary interactions. Additionally, Novoplansky's (2009) framework on adaptive competitive strategies underscores this perspective, suggesting that plants strategically modulate competition or cooperation based on neighbor traits, enhancing productivity only when functional diversity reduces direct resource overlap.

Remarkably, despite significant overall biomass increases under warming, observed equally in shoots and roots, the shoot-to-root (S:R) ratio remained unchanged. This aligns with recent findings from Dietrich et al. (2025), who reported stable biomass allocation patterns in response to enhanced nutrient availability under climatic gradients. According to optimal partitioning theory (van Noordwijk et al., 1998; Dietrich et al., 2025), this balanced allocation suggests plants proportionally enhanced both photosynthetic capacity aboveground and nutrient uptake belowground in response to warming-driven increases in nutrient availability. However, the assumption of enhanced microbial nutrient cycling completely alleviating nutrient constraints under warming deserves nuanced consideration. It is plausible that plants initially benefited from increased microbial nutrient cycling, facilitating early growth increments (Melillo et al., 2011; Allison & Treseder, 2008). Yet, as plants grew larger, increased nutrient demands potentially depleted soil nutrient pools by the time of harvesting, reflected in decreased Root Nitrogen Content (RNC). Furthermore, given that the ambient temperature conditions are suboptimal for growth of these species, warming may have facilitated more optimal physiological conditions, enhancing metabolic processes such as cell division and expansion, independently of sustained improvements in soil nutrient availability (Way & Oren, 2010). Therefore, stable S:R ratios and biomass increments likely reflect a combined effect of transient microbial-mediated nutrient availability and improved physiological growth conditions rather than continuous alleviation of nutrient limitation.

4.3 Mycorrhizal colonization patterns across temperature and mixture types

The third hypothesis posited that mycorrhizal colonization would be highest in single-species treatments, reflecting greater carbon allocation toward fungal symbionts under strong intraspecific nutrient competition. In contrast, we expected lower colonization levels in species mixtures, where reduced niche overlap would lessen the need for fungal-mediated nutrient acquisition. This hypothesis was not supported. Species identity, rather than warming treatment, was the predominant driver of colonization patterns, with birch monocultures having the highest percentage mycorrhizal colonization, and larch the lowest. This aligns well with observed symbiotic affinities in birches (Ostonen et al., 2011; Wang et al., 2021). Interestingly, in four species mixtures we observed significantly enhanced colonization relative to monocultures. It is possible that species mixtures reduce competitive intensity through fungal networks and by facilitating resource partitioning (van der Heijden et al., 2015; Simard et al., 2012; Clemmensen et al., 2015). Conversely, some functionally similar mixtures (e.g. larch and pine) experienced lower colonization, likely due to intensified competitive pressures arising from overlapping resource acquisition strategies.

Surprisingly, mycorrhizal colonization was remarkably stable under moderate warming (+3°C), contradicting initial expectations based on predicted shifts in nutrient mineralization and plant-fungal exchanges under warming (Mohan et al., 2014; Bennett & Classen, 2020). The observed resilience of ectomycorrhizal colonization under moderate warming conditions in our study mirrors findings by Dietrich et al. (2025), who reported species-specific stability in ectomycorrhizal colonization despite varying nitrogen deposition and climatic regimes. Notably, their study identified that increased nutrient availability from elevated nitrogen deposition reduced mycorrhizal colonization only when nitrogen availability exceeded a critical threshold, diminishing fungal carbohydrate allocation. This mechanism potentially explains our observed colonization stability, suggesting our moderate warming (+3°C) scenario likely did not exceed nutrient availability thresholds required to induce significant shifts in fungal-plant carbon dynamics (Dietrich et al., 2025; Deveau et al., 2018). This is despite lower nutrient availability observed in this study with warming. Interestingly, earlier observed conservative root trait adjustments, average root diameter (AD), a proxy for fungal accommodation capacity, did not differ across mixture treatments. This suggests that colonization could be more related to carbon availability, rather than anatomical constraints. These findings are consistent with recent evidence highlighting that mycorrhizal colonization is responsive to nutrient context and biotic interactions rather than solely to structural root traits (Freschet et al., 2021; Matthus et al., 2025).

Speculatively, higher warming intensities could still reduce colonization by alleviating nutrient competition, diminishing the necessity of fungal-mediated nutrient acquisition (Terrer et al., 2016; Pena & Tibbett, 2024). Under these conditions the sensitivity of mycorrhizal associations to community composition and root competition, while suggesting a degree of resilience to moderate warming. These insights point toward an emerging principle: in functionally diverse mixtures, reduced reliance on symbiotic outsourcing may free up carbon for aboveground growth, enhancing productivity without compromising nutrient uptake (Clemmensen et al., 2015; Fernandez et al., 2016; de Carlan et al., 2024).

4.4 Forest ecosystem implications (Conclusions)

This study advances our understanding of how elevated temperature influences root trait expression, biomass production, and mycorrhizal interactions in boreal tree seedlings. Through controlled climate chamber experimentation, we isolated moderate warming effects on early-stage seedling development, revealing patterns that challenge conventional assumptions in plant functional ecology.

Contrary to our initial hypothesis, warming did not shift root traits toward acquisitive strategies. Instead, a consistent transition across species toward conservative, structurally reinforced phenotypes emerged, characterized by reductions in specific root length (SRL), root nitrogen (RN), and specific root area (SRA), alongside increases in root carbon content (RCC) and C:N ratio. These responses likely reflect resource scarcity due to progressive nutrient depletion in a closed experimental system, highlighting temperature’s ability to override anticipated nutrient enrichment effects. Thus, our findings challenge the generalized expectation that warming universally promotes acquisitive trait expression, underscoring the critical role of environmental context in trait plasticity.

An additional speculative yet logically grounded explanation for the observed shift towards conservative root traits is related to the crucial importance of root development in seedling survival. Unlike mature trees, seedlings inherently prioritize developing strong, structurally robust root systems to maximize survival chances during vulnerable early life stages (Comas et al., 2013). The observed decrease in SRL and increase in root carbon content (RCC) likely represent an inherent developmental strategy that favors stable, dense, and potentially longerlived root structures (Freschet et al., 2018). Although we did not directly measure rooting depth or angles, this conservative trait constellation aligns with established literature suggesting deeper rooting potential under nutrient stress or warming conditions (Matthus et al., 2025; Weemstra et al., 2016). Lower SRL combined with increased RCC is often linked to deeper soil exploration and enhanced mechanical strength, crucial for seedlings encountering compacted or resource-limited soils (Weemstra et al., 2016). Therefore, while our experimental setup inherently limits the direct evaluation of rooting depth (McCormack & Iversen, 2019), the trait responses observed suggest that seedling roots strategically adopt conservative traits early on to enhance long-term survival.

In line with our second hypothesis, biomass overyielding occurred under warming in functionally diverse mixtures, particularly spruce–birch and four-species combinations, while functionally redundant mixtures did not benefit. Shoot-to-root ratios remained stable, suggesting coordinated allocation responses to warming. These results support the view that functional complementarity, rather than species richness alone, drives productivity gains under climate change.

Mycorrhizal colonization remained stable across temperature treatments and was governed primarily by species identity and mixture composition. That stability suggests trees maintained their partnership and were still functionally relevant, under moderate climate perturbations, likely operating within threshold dynamics where only severe changes in nutrient availability substantially alter symbiotic dynamics.

Overall, these findings emphasize that boreal tree seedlings' performance arises from complex interactions between genetic predispositions, environmental factors, and community context. Trait expression is not fixed but modulated by temperature, resource availability, competition, and biotic interactions (Nicotra et al., 2010; Sultan, 2000; Brundrett & Tedersoo, 2018). Importantly, the patterns observed - conservative root shifts, stable colonization, and biomass gains in mixtures, illustrate that warming can alter developmental trajectories in ways not always aligned with theoretical predictions.

Importantly, our study manipulated one variable - temperature, in isolation, within a closed pot system. As recent studies emphasize (in ‘t Zandt et al., 2025; Münzbergová et al., 2017), plant responses to climate are shaped by the interplay of temperature, moisture, soil chemistry, and seasonal timing. Moreover, root trait plasticity and mycorrhizal interactions are genetically and environmentally driven, they may also carry transgenerational influences shaped by maternal environments (Münzbergová & Hadincová, 2017). These factors were not measured in this experiment and may help explain some of the variability observed in our results. To fully inform future forest management strategies, there is room for more research on single factor experiments and embrace multifactorial approaches. This includes tracking seedling performance across gradients of CO_2, water availability, nutrients, humidity, and soil conditions, alongside measurements of individual growth trajectories, rooting depth, phenology, pH, and community-level interactions. Then we can get the complete picture and accurately project how forest regeneration and productivity will unfold under future climate scenarios.

4.5 Ecological and silvicultural implications

From a forestry perspective, the observed increase in total biomass under warming suggests that elevated temperatures, within moderate limits - could be strategically leveraged in nursery or early-establishment phases to accelerate seedling growth. This study underscores that boreal forest productivity under climate change will depend not only on temperature effects but on the interplay of species traits, environmental variability, and biotic variables. By integrating trait-based insights into forest planning, we can move toward more adaptive, ecologically informed strategies for future silviculture.

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Popular science summary

Climate change is warming boreal forests faster than many other parts of the world. In northern Sweden, rising temperatures may change how tree roots grow and how trees interact underground. But how exactly do young trees adapt their root systems and partnerships with helpful soil fungi when the soil gets warmer? And can planting different tree species together make forests grow better in the future?

To answer this, we studied seedlings of four common or potentially important boreal tree species: spruce, pine, birch, and Siberian larch. These were grown either alone or in combinations, in soil kept at normal (15°C) or warmer (18°C) temperatures. After five months, we measured root traits, fungal colonization, and biomass to see how warming and species mixing affected their growth and behavior belowground.

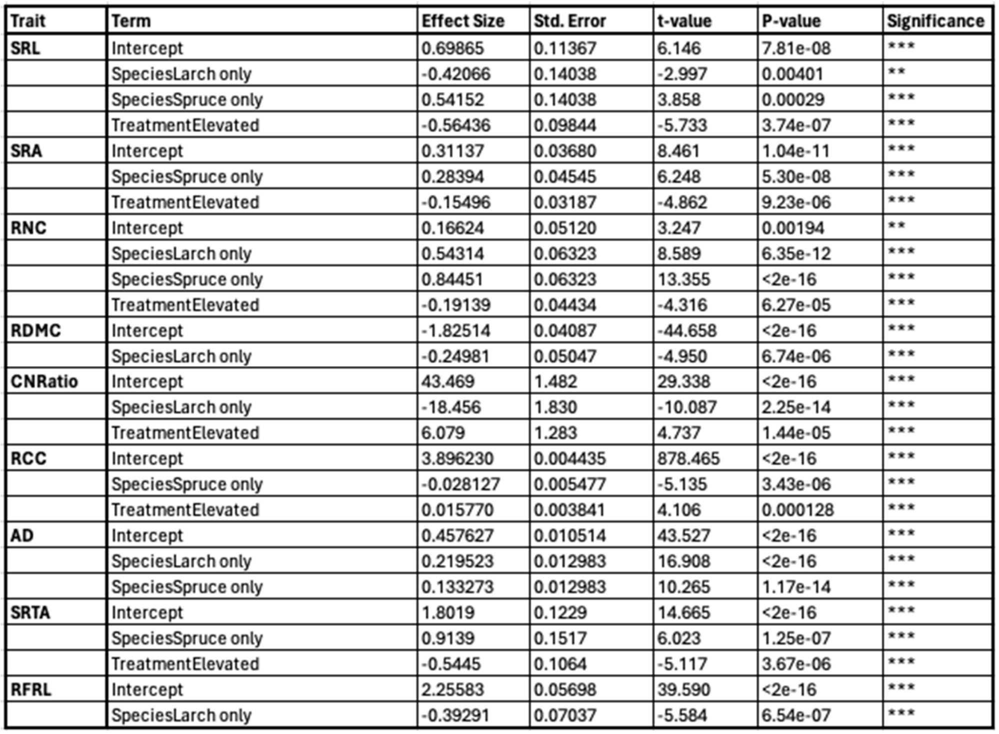
Surprisingly, warming did not make roots more “greedy” for nutrients, as expected. Instead, the seedlings invested in sturdier, longer-lasting roots, a strategy more about survival than fast growth. Even more interestingly, we found that mixed-species pots produced more total biomass than single-species pots, especially under warmer conditions. This suggests that when trees with different strategies grow together, they can share resources more efficiently and grow better as a group.

Helpful root fungi, called ectomycorrhizae - were more common in birch and lowest in larch, and did not decrease with warming as expected. This shows that tree-fungal partnerships can remain stable and functionally relevant, even as temperatures rise.

These findings suggest that promoting species diversity in forests may help young trees thrive in a warmer climate, and further studies is needed with similar approach. Will offering insights for more resilient and productive forest management in Sweden and beyond.

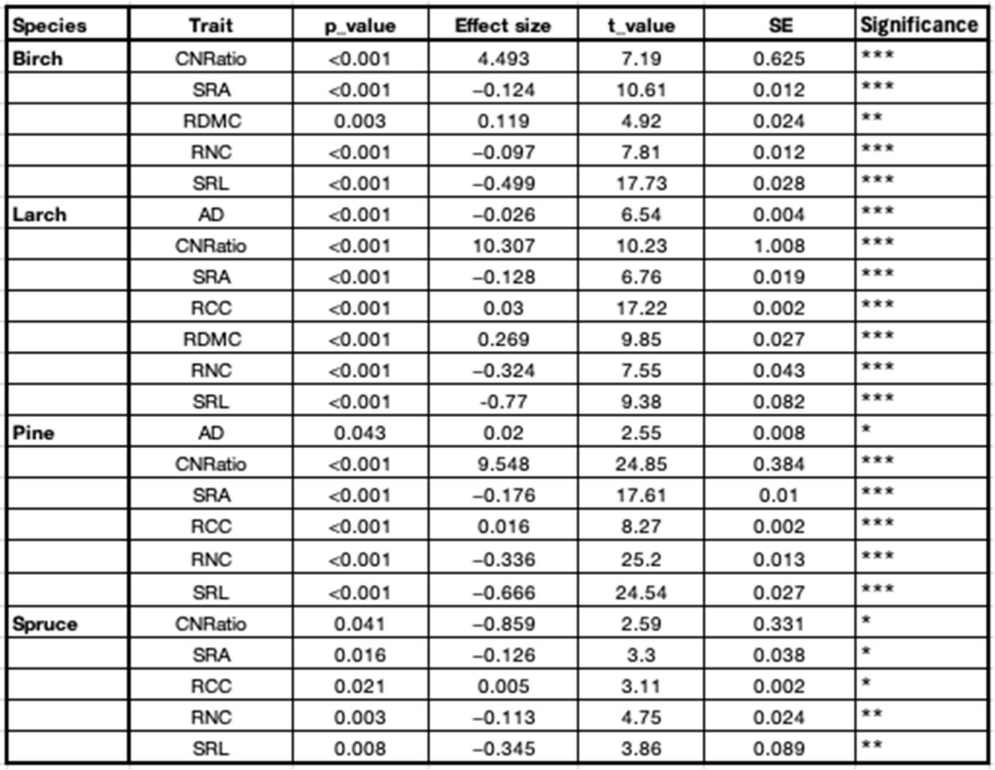
Supplementary data

*Table S1. Only significant summarizes the fixed effect estimates from the Linear Mixed-Effects Model (LMM) analyzing the influence of species identity and temperature on fine root traits. For each trait estimates, standard errors, degrees of freedom, t-values, and p-values are provided. Significant species effects (p < 0.001) are highlighted. Asterisks indicate statistical significance (***, P ≤ 0.001; **, P ≤ 0.01; *, P ≤ 0.05;)., and treatment effects are reported. Random effects for Block (variance = 31.23) and residual variance are also included to account for variation across experimental units. The P-values and significance markers confirm several patterns observed in previous statistical analyses, aligning with the PCA, RDA, and post-hoc comparisons. That species identity is a dominant factor in shaping root trait shifts under warming, while temperature effects remain consistent across species.*

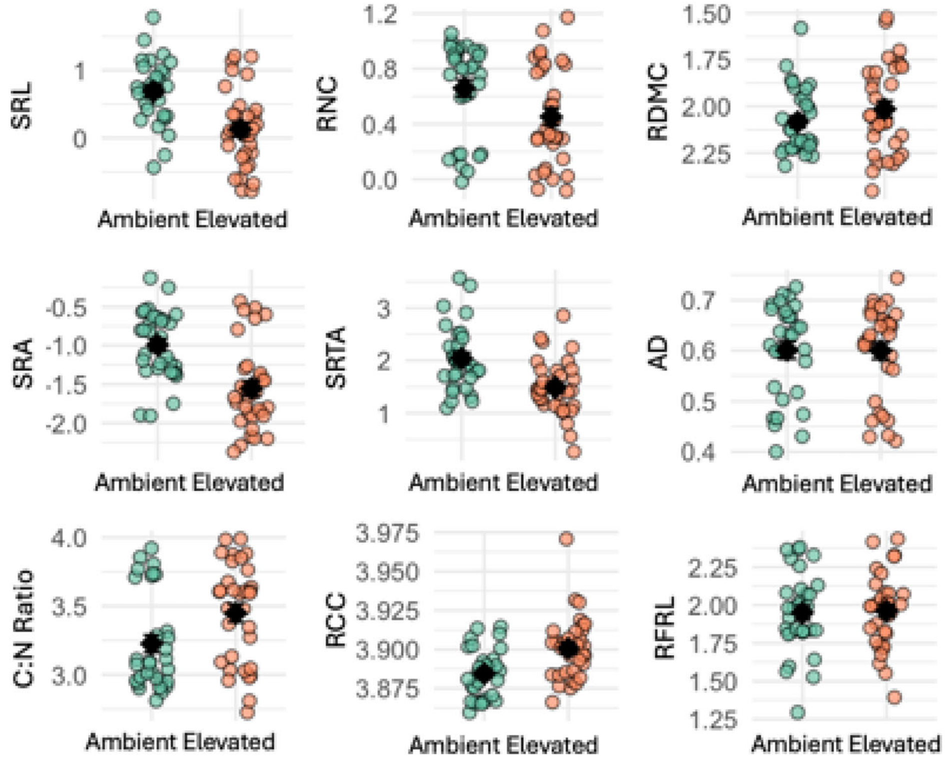


Trait	Term	Effect Size	Std. Error	t-value	P-value	Significance
SRL	Intercept	0.69865	0.11367	6.146	7.81e-08	***
	SpeciesLarch only	-0.42066	0.14038	-2.997	0.00401	**
	SpeciesSpruce only	0.54152	0.14038	3.858	0.00029	***
	TreatmentElevated	-0.56436	0.09844	-5.733	3.74e-07	***
SRA	Intercept	0.31137	0.03680	8.461	1.04e-11	***
	SpeciesSpruce only	0.28394	0.04545	6.248	5.30e-08	***
	TreatmentElevated	-0.15496	0.03187	-4.862	9.23e-06	***
RNC	Intercept	0.16624	0.05120	3.247	0.00194	**
	SpeciesLarch only	0.54314	0.06323	8.589	6.35e-12	***
	SpeciesSpruce only	0.84451	0.06323	13.355	<2e-16	***
	TreatmentElevated	-0.19139	0.04434	-4.316	6.27e-05	***
RDMC	Intercept	-1.82514	0.04087	-44.658	<2e-16	***
	SpeciesLarch only	-0.24981	0.05047	-4.950	6.74e-06	***
CNRatio	Intercept	43.469	1.482	29.338	<2e-16	***
	SpeciesLarch only	-18.456	1.830	-10.087	2.25e-14	***
	TreatmentElevated	6.079	1.283	4.737	1.44e-05	***
RCC	Intercept	3.896230	0.004435	878.465	<2e-16	***
	SpeciesSpruce only	-0.028127	0.005477	-5.135	3.43e-06	***
	TreatmentElevated	0.015770	0.003841	4.106	0.000128	***
AD	Intercept	0.457627	0.010514	43.527	<2e-16	***
	SpeciesLarch only	0.219523	0.012983	16.908	<2e-16	***
	SpeciesSpruce only	0.133273	0.012983	10.265	1.17e-14	***
SRTA	Intercept	1.8019	0.1229	14.665	<2e-16	***
	SpeciesSpruce only	0.9139	0.1517	6.023	1.25e-07	***
	TreatmentElevated	-0.5445	0.1064	-5.117	3.67e-06	***
RFRL	Intercept	2.25583	0.05698	39.590	<2e-16	***
	SpeciesLarch only	-0.39291	0.07037	-5.584	6.54e-07	***

*Table S2. summarizes the paired t-test estimates analyzing species-specific fine root trait shifts under warming. The table provides mean differences, standard errors, degrees of freedom (df = 6), t-values, and p-values for each trait comparison. Asterisks indicate statistical significance (***, P ≤ 0.001; **, P ≤ 0.01; *, P ≤ 0.05;). The results confirm species-level variation in root trait adjustments, supporting broader findings from ANOVA, PCA, RDA, and post-hoc comparisons that warming influences root functional strategies across species.*



Species	Trait	p_value	Effect size	t_value	SE	Significance
Birch	CNRatio	<0.001	4.493	7.19	0.625	***
	SRA	<0.001	−0.124	10.61	0.012	***
	RDMC	0.003	0.119	4.92	0.024	**
	RNC	<0.001	−0.097	7.81	0.012	***
	SRL	<0.001	−0.499	17.73	0.028	***
Larch	AD	<0.001	−0.026	6.54	0.004	***
	CNRatio	<0.001	10.307	10.23	1.008	***
	SRA	<0.001	−0.128	6.76	0.019	***
	RCC	<0.001	0.03	17.22	0.002	***
	RDMC	<0.001	0.269	9.85	0.027	***
	RNC	<0.001	−0.324	7.55	0.043	***
	SRL	<0.001	-0.77	9.38	0.082	***
Pine	AD	0.043	0.02	2.55	0.008	*
	CNRatio	<0.001	9.548	24.85	0.384	***
	SRA	<0.001	−0.176	17.61	0.01	***
	RCC	<0.001	0.016	8.27	0.002	***
	RNC	<0.001	−0.336	25.2	0.013	***
	SRL	<0.001	−0.666	24.54	0.027	***
Spruce	CNRatio	0.041	−0.859	2.59	0.331	*
	SRA	0.016	−0.126	3.3	0.038	*
	RCC	0.021	0.005	3.11	0.002	*
	RNC	0.003	−0.113	4.75	0.024	**
	SRL	0.008	−0.345	3.86	0.089	**



Fgure S1: Root trait responses to temperature treatments (Ambient vs Elevated). Multi-panel boxplots showing individual root trait distributions under ambient (green) and elevated (orange) temperatures across all species. Traits include morphological (SRL, SRA, RDMC, AD, SRTA, RFRL) and chemical (RNC, RCC, CNRatio) indicators. Significant decreases were observed under warming for SRL, SRA, SRTA, and RNC, while RCC and CNRatio increased (see Table 1). Non-significant traits included AD and RFRL. Black points represent group means. This figure supports the overall trend toward conservative root trait expression under warming.


A
Species-Specific **SRL** Responses
SRL (cm / mg^{-1})
1
0
Ambient
Elevated
Treatment
B
Species-Specific **SRA** Responses
SRA (cm^2 / mg^{-1})
0.75
0.50
0.25
Ambient
Elevated
Treatment
C
Species-Specific **RNC** Responses
RNC (%)
1.2
0.8
0.4
0.0
Ambient
Elevated
Treatment
D
Species-Specific **RDMC** Responses
RDMC (mg / mg^{-1})
-1.50
-1.75
-2.00
-2.25
Ambient
Elevated
Treatment
E
Species-Specific **C:N Ratio** Responses
C:N Ratio
50
40
30
20
Ambient
Elevated
Treatment
Species
Birch only
Larch only
Pine only
Spruce only

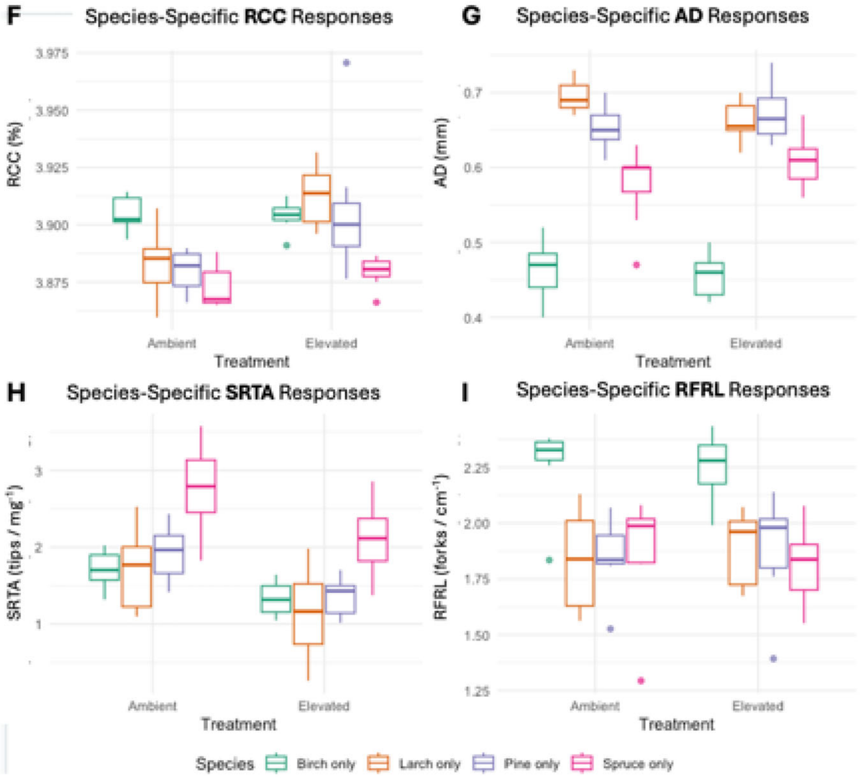

F
Species-Specific **RCC** Responses
RCC (%)
3.975
3.950
3.925
3.900
3.875
Ambient
Elevated
Treatment
G
Species-Specific **AD** Responses
AD (mm)
0.7
0.6
0.5
0.4
Ambient
Elevated
Treatment
H
Species-Specific **SRTA** Responses
SRTA (tips / mg^{-1})
3
2
1
Ambient
Elevated
Treatment
I
Species-Specific **RFRL** Responses
RFRL (forks / cm^{-1})
2.25
2.00
1.75
1.50
1.25
Ambient
Elevated
Treatment
Species
Birch only
Larch only
Pine only
Spruce only

Figure S2 Boxplots display species-specific responses of fine root traits under ambient and elevated temperature treatments. Panels illustrate:

(A) Specific Root Length (SRL, mm mg^{-1}*)*

(B) Specific Root Area (SRA, mm^2 mg^{-1}*)*

(C) Root Nitrogen Content (RNC, %)

(D) Root Dry Matter Content (RDMC, % ELLER mg mg^{-1}*)*

(E) Carbon-to-Nitrogen Ratio (CNRatio)

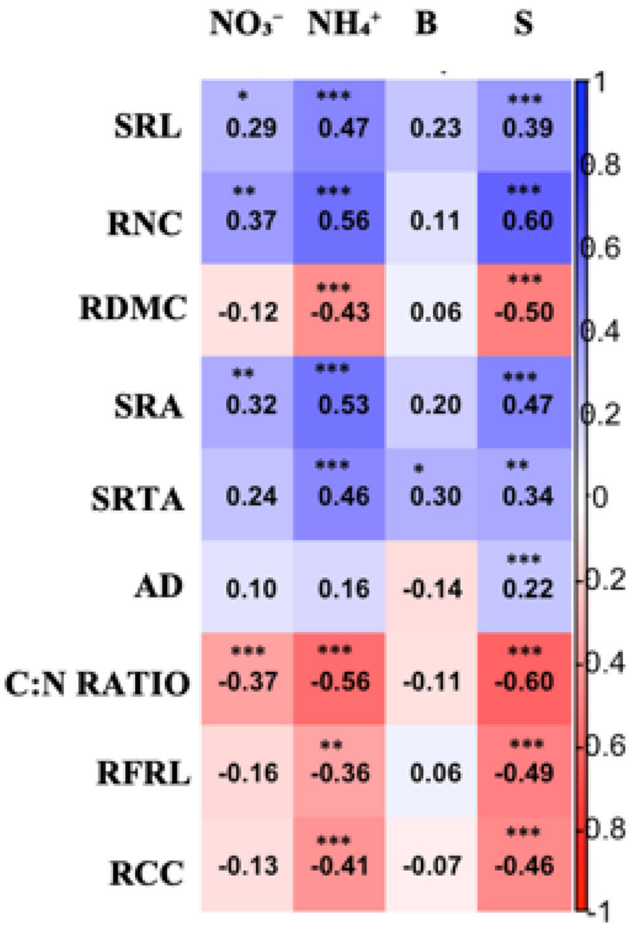
(F) Root Carbon Content (RCC, %)

(G) Average Diameter (AD, mm)

(H) Specific Root Tip Abundance (SRTA,tips mm^2 *mg)*

(I) Root Fork Tip (RFRL, forks mm/mg)

Data points represent individual species-treatment measurements. Boxplots show median, interquartile range (IQR), and outliers, highlighting trait shifts under warming.



	NO_3^-	NH_4^+	B	S
SRL	* 0.29	*** 0.47	0.23	*** 0.39
RNC	** 0.37	*** 0.56	0.11	*** 0.60
RDMC	-0.12	*** -0.43	0.06	*** -0.50
SRA	** 0.32	*** 0.53	0.20	*** 0.47
SRTA	0.24	*** 0.46	* 0.30	** 0.34
AD	0.10	0.16	-0.14	*** 0.22
C:N RATIO	*** -0.37	*** -0.56	-0.11	*** -0.60
RFRL	-0.16	** -0.36	0.06	*** -0.49
RCC	-0.13	*** -0.41	-0.07	*** -0.46

*Figure S3: Heatmap of Pearson correlation coefficients between log-transformed root traits and significant soil nutrients (NO_3^-, NH_4^+, B, S). Strong positive correlations (blue) were found between acquisitive traits (SRL, SRA, RNC, SRTA) and NH_4^+ or NO_3^-. Conservative traits (CNRatio, RDMC, RCC) showed strong negative correlations (red) with the same nutrients. Non-significant associations (e.g., AD) appear near-neutral. This supports the interpretation that nutrient scarcity under warming promoted conservative trait expression. (Asterisks indicate statistical significance (***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$;)*

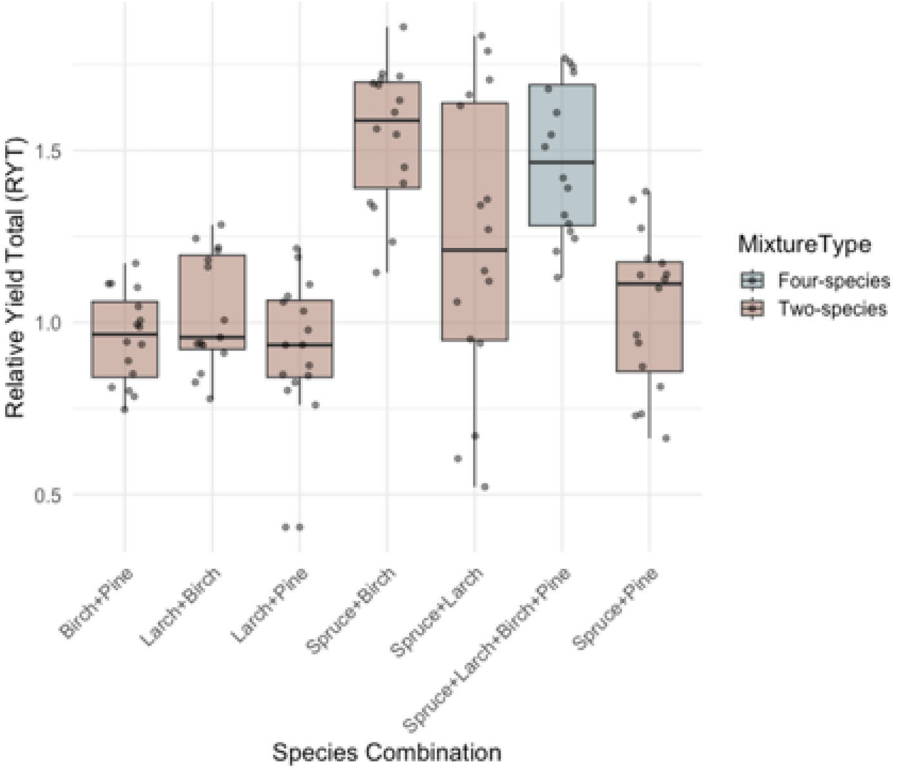


Figure S4. Relative Yield Total (RYT) across different two-species and four-species combinations under ambient and elevated temperatures. RYT was calculated as the sum of the observed-to-monoculture yield ratios for each species (see Methods). ANOVA results showed significant effects of mixture type ($p < 1.63e-06$) and temperature ($p < 2.48e-10$), but the interaction between mixture type and temperature was not significant ($p = 0.698$). Tukey's HSD post-hoc tests confirmed significant overyielding ($p < 0.05$) in Spruce + Birch and the four-species mixture, while Larch + Pine and Birch + Pine exhibited underyielding ($p > 0.05$). Data points represent individual RYT values for each species combination.

*Table S3. Effects of elevated temperature on biomass metrics across different mixture types (single-species, two-species, and four-species). Results are shown for total biomass, average height, shoot biomass, root biomass, and fine root biomass. F-values and p-values were obtained from ANOVA models conducted separately within each mixture type. Elevated temperature significantly increased all biomass metrics across all mixture types. Significance levels are indicated by asterisks: ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$.*

Response variable	Mixture Type	Species / Mixture Type	Test statistic	p-value	Significance
Total biomass	Mixture Type: Single-species	Single-species	F = 26.22	< 0.001	***
	Mixture Type: Two-species	Two-species	F = 50.49	< 0.001	***
	Mixture Type: Four-species	Four-species	F = 62.82	< 0.001	***
	Birch only	Single-species	F = 14.52	0.001	**
	Larch only	Single-species	F = 26.34	< 0.001	***
	Pine only	Single-species	F = 29.78	< 0.001	***
	Spruce only	Single-species	F = 6.35	0.0217	*
	Birch+Pine	Two-species	F = 13.51	< 0.001	***
	Larch+Pine	Two-species	F = 9.64	0.009	**
	Spruce+Larch	Two-species	F = 17.56	< 0.001	***
	Spruce+Birch	Two-species	F = 13.72	0.002	**
	Spruce+Pine	Two-species	F = 18.23	< 0.001	***
	Larch+Birch	Two-species	F = 51.41	< 0.001	***
	Spruce+Larch+Birch+Pine	Four-species	F = 62.82	< 0.001	***
Avg Height	Mixture Type: Single-species	Single-species	F = 18.34	< 0.001	***
	Mixture Type: Two-species	Two-species	F = 27.49	< 0.001	***
	Mixture Type: Four-species	Four-species	F = 24.35	< 0.001	***
	Birch only	Single-species	F = 9.51	0.008	**
	Larch only	Single-species	F = 11.30	0.0046	**
	Spruce only	Single-species	F = 14.61	0.0018	**
	Pine only	Single-species	F = 9.72	0.0076	**
	Spruce+Birch	Two-species	F = 16.52	0.0012	**
	Larch+Birch	Two-species	F = 6.41	0.0239	*
	Spruce+Larch	Two-species	F = 10.68	0.0061	**
	Spruce+Pine	Two-species	F = 5.56	0.0334	*
	Larch+Pine	Two-species	F = 3.68	0.0757	
	Birch+Pine	Two-species	F = 2.10	0.169	
	Spruce+Larch+Birch+Pine	Four-species	F = 24.35	< 0.001	***
Shoot Biomass	Mixture Type: Single-species	Single-species	F = 32.10	< 0.001	***
	Mixture Type: Two-species	Two-species	F = 46.37	< 0.001	***
	Mixture Type: Four-species	Four-species	F = 37.70	< 0.001	***
	Birch only	Single-species	F = 13.30	0.001	**
	Larch only	Single-species	F = 14.80	< 0.001	**
	Spruce only	Single-species	F = 11.50	0.004	**
	Pine only	Single-species	F = 64.38	< 0.001	***
	Spruce+Birch	Two-species	F = 18.89	< 0.001	***
	Larch+Birch	Two-species	F = 22.00	< 0.001	***
	Spruce+Larch	Two-species	F = 46.37	< 0.001	***
	Spruce+Pine	Two-species	F = 12.50	0.004	**
	Larch+Pine	Two-species	F = 20.12	< 0.001	***
	Birch+Pine	Two-species	F = 23.50	< 0.001	***
	Spruce+Larch+Birch+Pine	Four-species	F = 37.70	< 0.001	***
Root biomass	Mixture Type: Single-species	Single-species	F = 26.19	< 0.001	***
	Mixture Type: Two-species	Two-species	F = 33.71	< 0.001	***
	Mixture Type: Four-species	Four-species	F = 23.76	< 0.001	***
	Spruce only	Single-species	F = 8.27	0.012	*
	Larch only	Single-species	F = 11.90	0.004	**
	Birch only	Single-species	F = 11.35	0.005	**
	Pine only	Single-species	F = 34.33	< 0.001	***
	Spruce+Larch	Two-species	F = 18.39	< 0.001	***
	Spruce+Birch	Two-species	F = 23.84	< 0.001	***
	Spruce+Pine	Two-species	F = 11.53	0.004	**
	Larch+Birch	Two-species	F = 2.25	0.156	
	Larch+Pine	Two-species	F = 19.10	< 0.001	***
	Birch+Pine	Two-species	F = 21.31	< 0.001	***
	Spruce+Larch+Birch+Pine	Four-species	F = 23.76	< 0.001	***
Fine root biomass	Mixture Type: Single-species	Single-species	F = 21.96	< 0.001	***
	Mixture Type: Two-species	Two-species	F = 37.18	< 0.001	***
	Mixture Type: Four-species	Four-species	F = 18.58	< 0.001	***
	Spruce only	Single-species	F = 8.65	0.01	**
	Larch only	Single-species	F = 11.61	0.004	**
	Birch only	Single-species	F = 9.08	0.009	**
	Pine only	Single-species	F = 35.61	< 0.001	***
	Spruce+Larch	Two-species	F = 16.44	0.001	**
	Spruce+Birch	Two-species	F = 15.88	0.001	**
	Spruce+Pine	Two-species	F = 10.53	0.006	**
	Larch+Birch	Two-species	F = 15.97	0.001	**
	Larch+Pine	Two-species	F = 24.48	< 0.001	***
	Birch+Pine	Two-species	F = 23.21	< 0.001	***
	Spruce+Larch+Birch+Pine	Four-species	F = 18.58	< 0.001	***

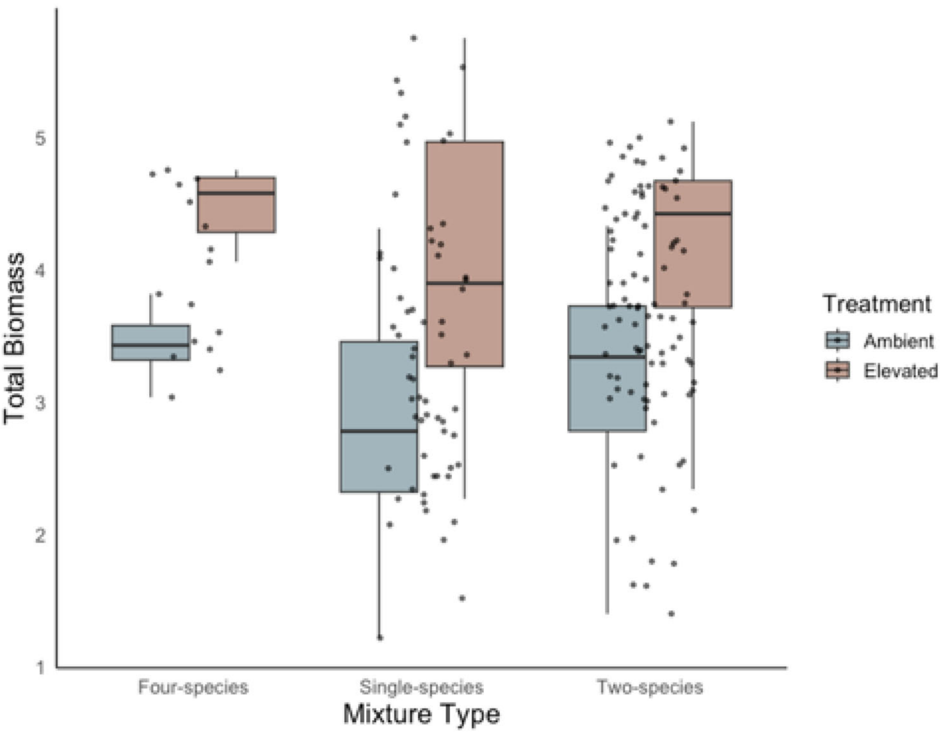


Figure S5. Total biomass (sum of shoot weight, root weight, and height, log-transformed) across single-species, two-species, and four-species mixtures under ambient (blue) and elevated (brown) temperature treatments. ANOVA results confirmed significant effects of temperature ($p < 0.001$) and species identity ($p < 0.001$), but the interaction was not significant ($p = 0.212$), indicating a general increase in biomass under warming. Post-hoc Tukey's HSD tests showed significant differences between single-species and mixed-species treatments ($p < 0.05$). Data points represent individual observations.

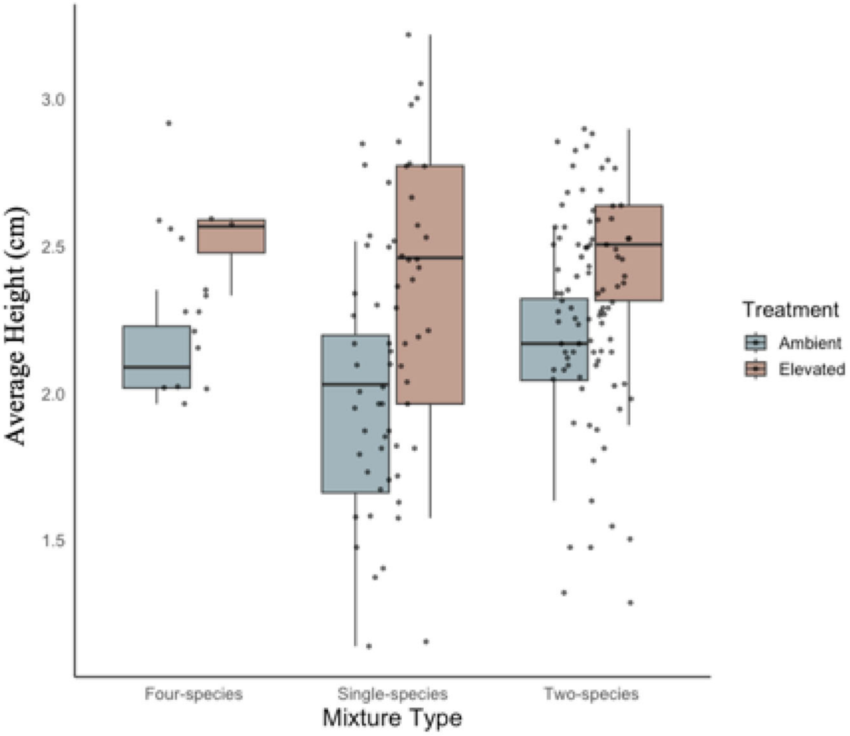


Figure S6A. Average seedling height (log-transformed) across single-species, two-species, and four-species mixtures under ambient (blue) and elevated (brown) temperatures. Data points represent individual observations.

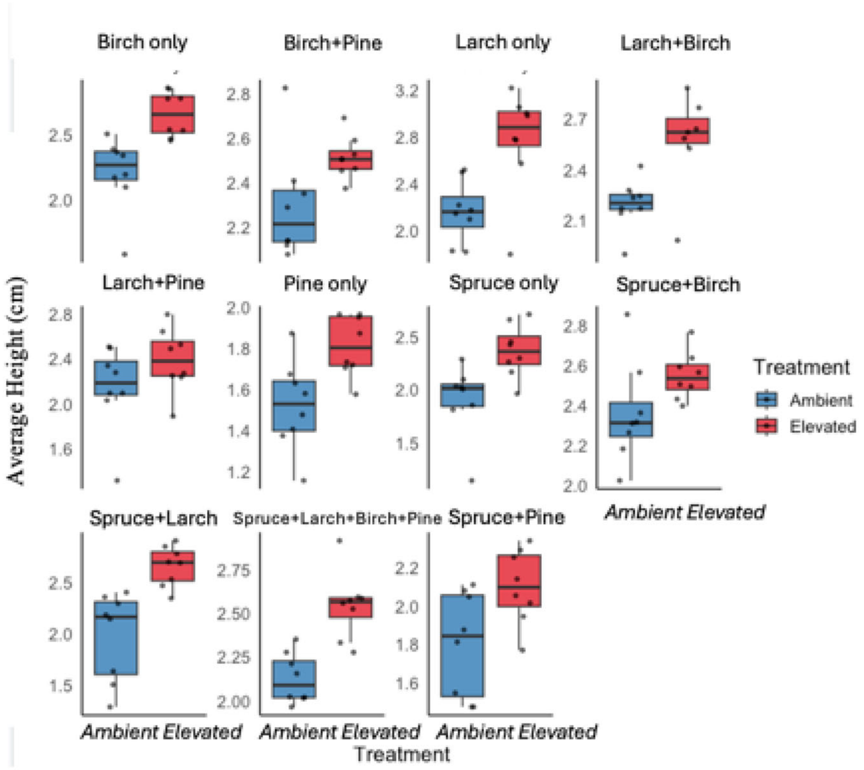


Figure S6B. Boxplots of log-transformed height for each species under ambient (blue) and elevated (red) temperature treatments. ANOVA showed significant temperature ($p < 0.001$) and species effects ($p < 0.001$), with Larch and Birch exhibiting the highest height increases under warming. Tukey's HSD tests confirmed significant treatment differences ($p < 0.05$). Data points represent individual replicates.

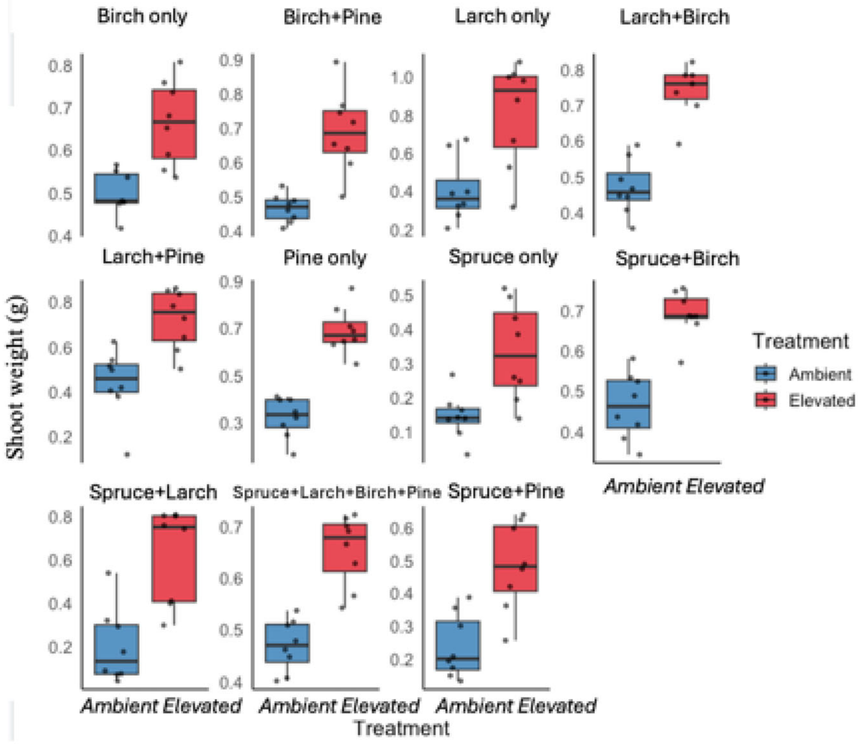


Figure S7. Boxplots illustrating shoot weight (log-transformed) for single- and mixed-species treatments under ambient (blue) and elevated (red) temperatures. ANOVA revealed a significant treatment effect ($p < 0.001$) and species effect ($p < 0.001$), with no significant species × treatment interaction ($p > 0.05$). Post-hoc Tukey's HSD tests indicated significant differences in shoot biomass allocation across species ($p < 0.05$). Data points represent individual observations.

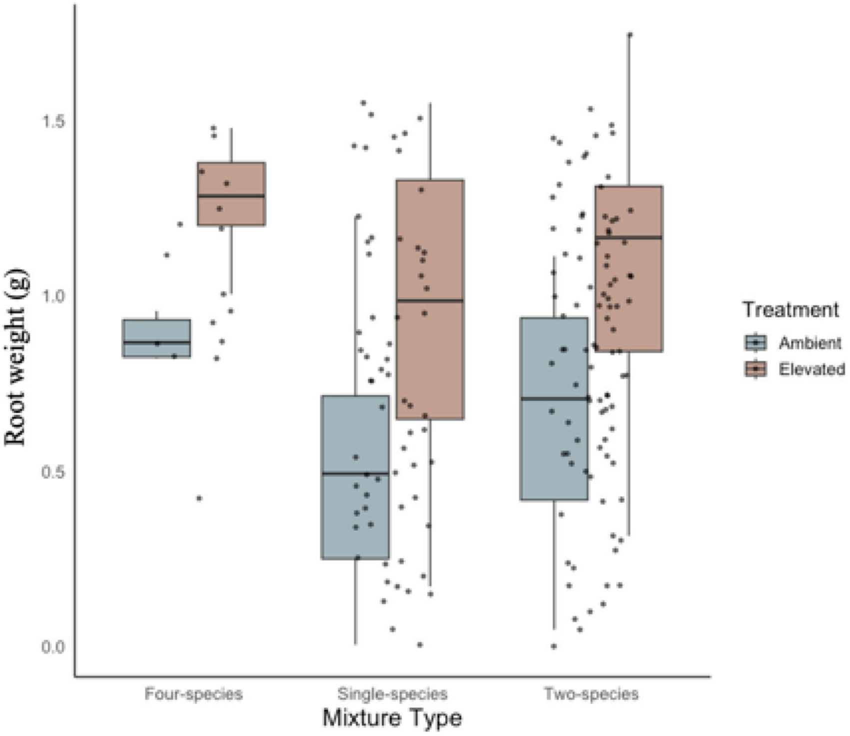


Figure S8A. Root biomass (log-transformed) across single-species, two-species, and four-species mixtures under ambient (blue) and elevated (brown) temperatures. ANOVA showed significant temperature ($p < 0.001$) and species effects ($p < 0.001$), but the interaction was not significant ($p > 0.05$). Post-hoc Tukey's HSD tests revealed significant increases in root biomass under warming, particularly in mixed-species treatments. Data points represent individual observations.

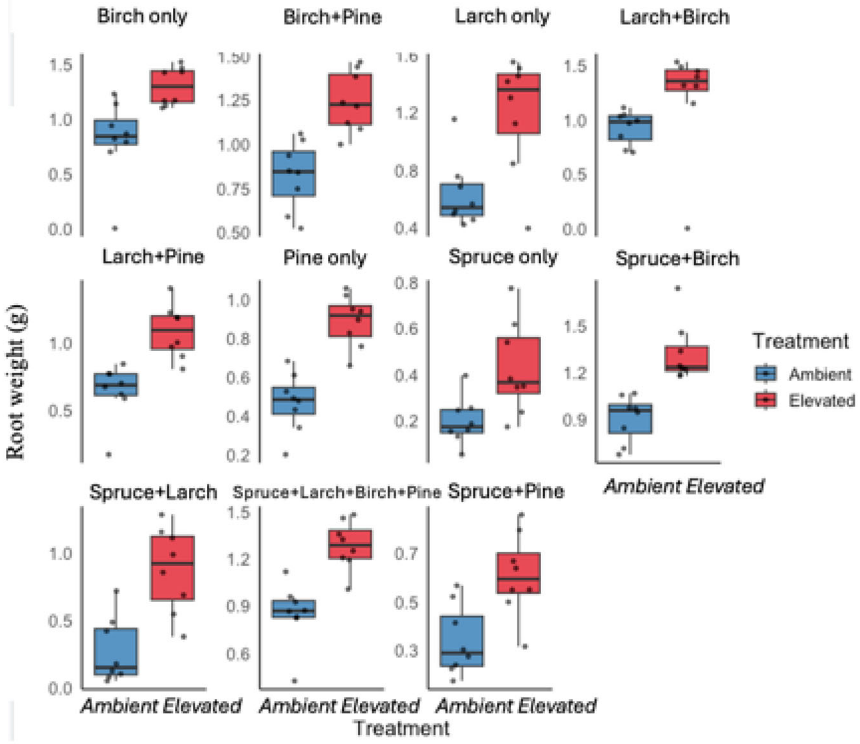


Figure S8B. Root biomass (log-transformed) across single- and mixed-species treatments under ambient (blue) and elevated (red) temperature treatments. ANOVA indicated significant temperature ($p < 0.001$) and species effects ($p < 0.001$), with species-specific variation in root biomass allocation. Tukey's HSD tests showed significant differences between species and treatments ($p < 0.05$). Data points represent individual replicates.

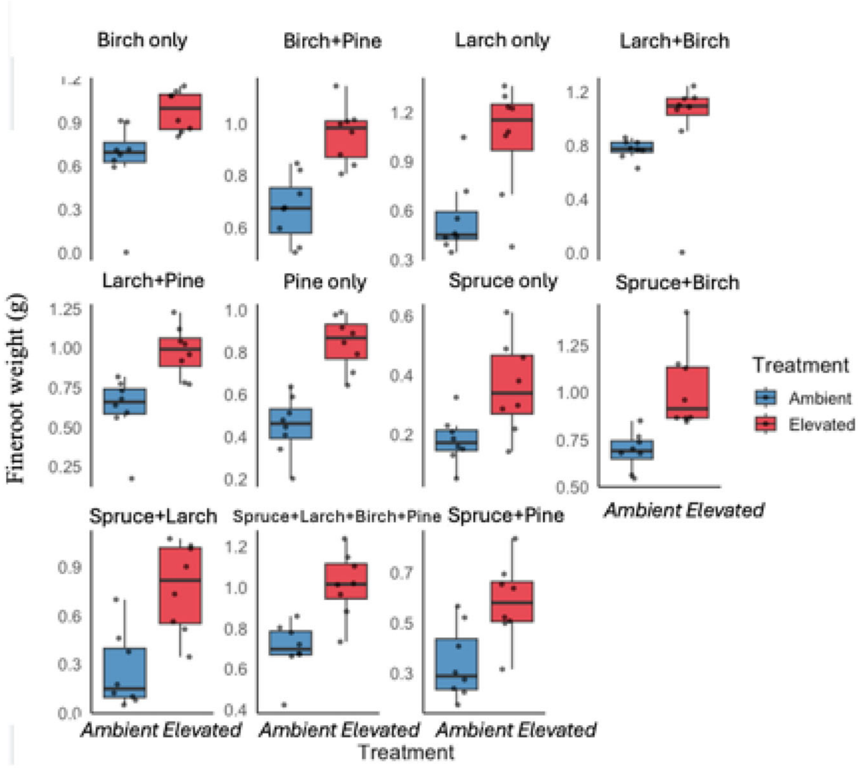


Figure S9A. Fine root biomass (log-transformed) across species under ambient (blue) and elevated (red) temperature treatments. ANOVA revealed significant temperature ($p < 0.001$) and species effects ($p < 0.001$), with fine root biomass significantly increasing in mixed-species treatments. Post-hoc Tukey's HSD tests confirmed significant treatment differences ($p < 0.05$). Data points represent individual samples.

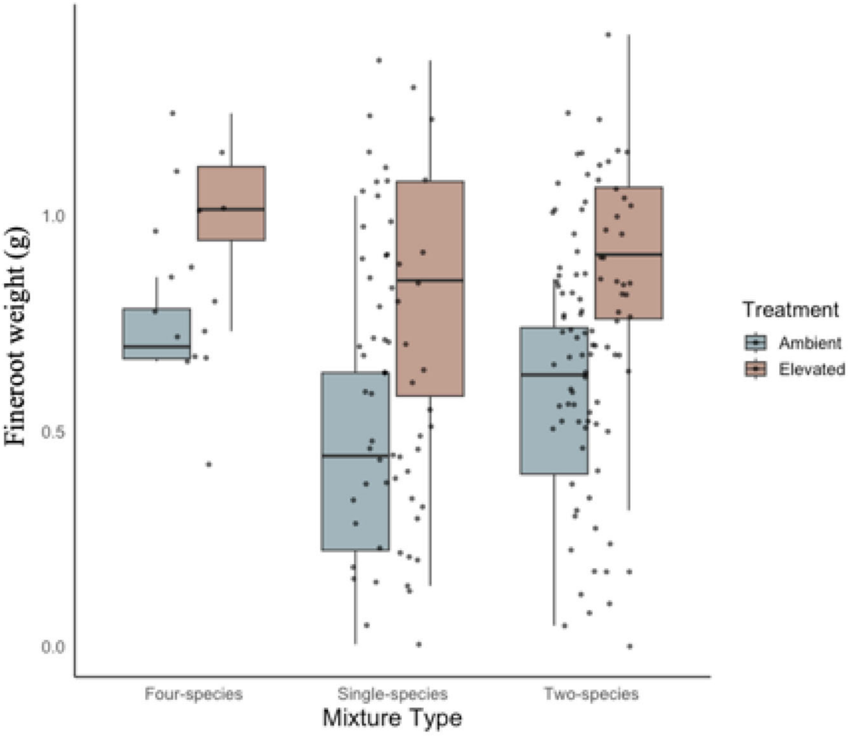


Figure S9B. Fine root biomass (log-transformed) across single-species, two-species, and four-species mixtures under ambient (blue) and elevated (brown) temperatures. Post-hoc Tukey's HSD tests confirmed that four-species mixtures exhibited the highest fine root biomass under elevated temperature (p = 0.0007, F = 18.58), suggesting that diverse species mixtures may enhance belowground biomass partitioning under climate change conditions. Data points represent individual observations.

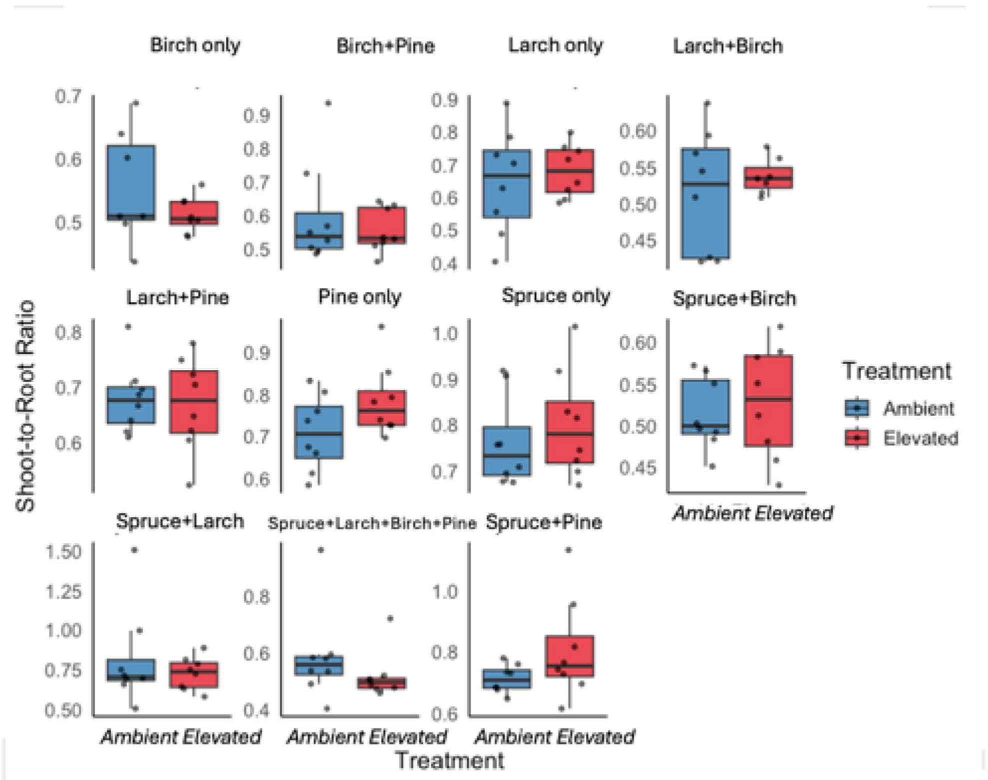


Figure S10A. Shoot-to-root ratio (S:R ratio) for individual species across ambient (blue) and elevated (red) temperature treatments. ANOVA results indicated significant species effects ($p < 2e-16$), with Spruce-only and Spruce+Larch mixtures displaying the highest S:R ratios, indicating a greater aboveground investment. Tukey's HSD tests showed that Spruce+Larch had significantly higher S:R than Larch+Pine ($p < 0.05$). Temperature effects were marginally significant ($p = 0.0471$), slightly decreasing root investment, but no significant species × temperature interaction was detected ($p = 0.3594$). Data points represent individual S:R ratio measurements for each species.

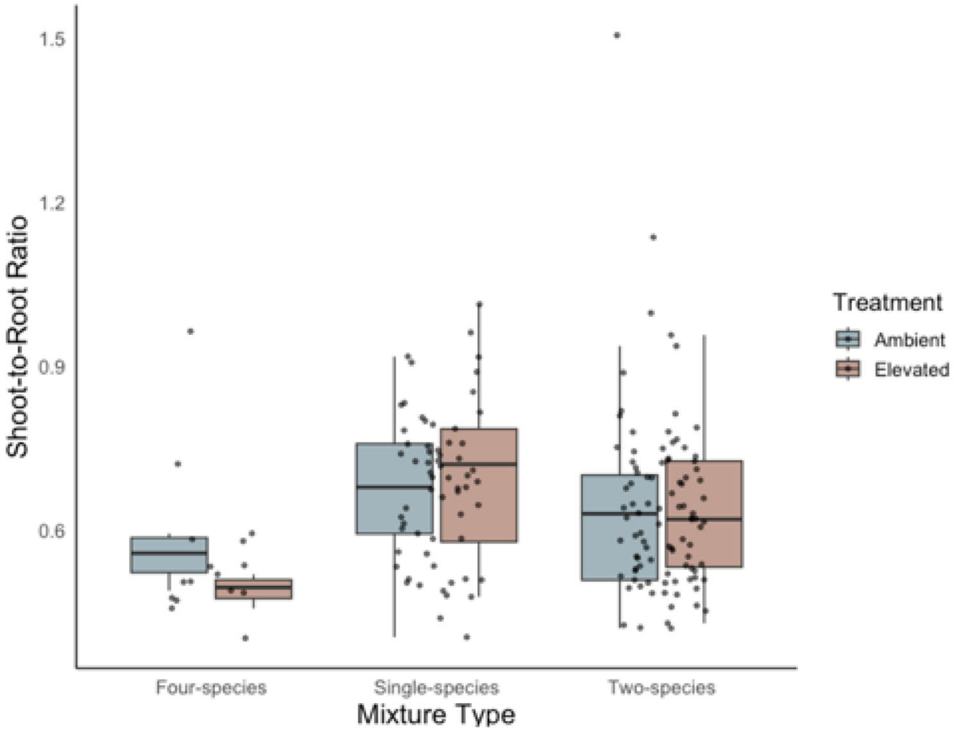


Figure S10B. Shoot-to-root ratio (S:R ratio) across single-species, two-species, and four-species mixtures under ambient (blue) and elevated (brown) temperatures. A higher S:R ratio indicates greater aboveground allocation, while a lower ratio suggests increased root investment. ANOVA results revealed significant species effects (p < 2e-16) but no significant temperature × mixture type interaction (p = 0.3594). Elevated temperature had a marginally significant effect (p = 0.0471), slightly reducing root investment. Data points represent individual S:R ratios for each sample.

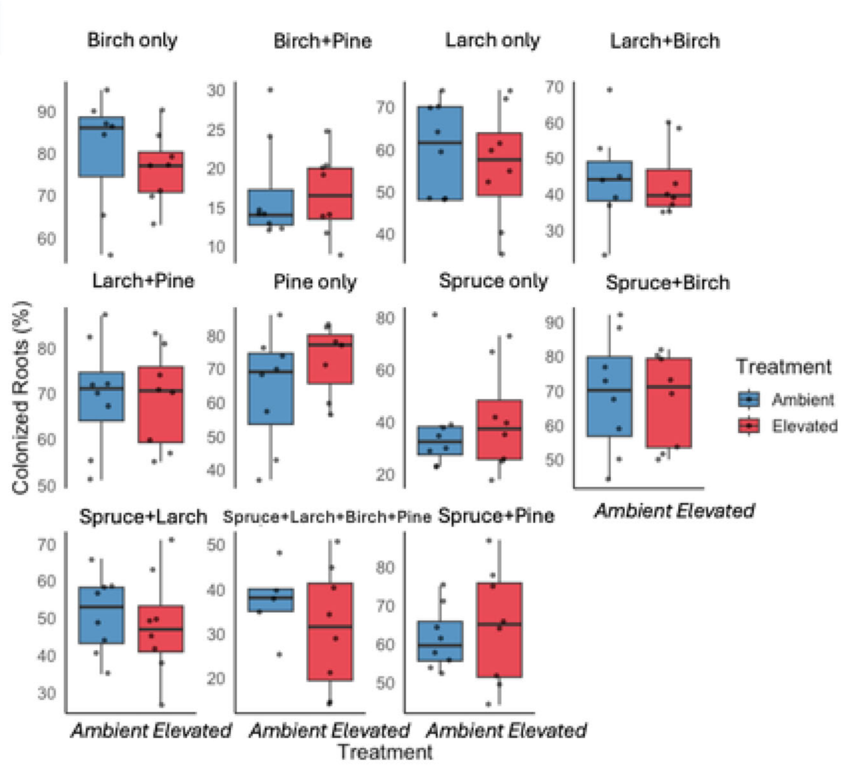


Figure S11. Species-specific mycorrhizal colonization rates under ambient (blue) and elevated (red) temperature treatments. ANOVA and LMM results confirmed that species identity was the primary driver of colonization (Chisq = 401.13, p < 2.2e-16), with block effects accounting for experimental variability but not altering significance. Temperature effects were not significant (p = 0.777). Pairwise Tukey's HSD comparisons showed that Birch-only treatments had the highest fungal associations, while Larch+Pine and Spruce+Larch exhibited lower colonization. Data points represent individual measurements for each species-treatment combination.

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